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Vol. 11: Physidae

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REVIEW OF LITERATURE ON ABIOTIC FACTORS INFLUENCING THE DISTRIBUTION AND LIFE CYCLES OF BILHARZIASIS INTERMEDIATE HOST SNAILS[1]

C. C. Appleton[2]

ABSTRACT

There is a profuse and often repetitive literature dealing with abiotic factors which have been thought to influence the distribution and life cycles of the bilharziasis intermediate host snails of the family Planorbidae. These snails, which belong to the genera *Bulinus* and *Biomphalaria*, are the intermediate hosts of *Schistosoma haematobium* (Bilharz), causing human urinary bilharziasis, and *S. mansoni* Sambon, causing human intestinal bilharziasis respectively. They are both endemic to Africa, and the latter also to South America. In many cases comparable findings have been recorded on both continents.

This paper collates and reviews the available literature and attempts to indicate those factors which are important in limiting host snail distribution and to expose those which merit further attention. Pertinent studies on other snail species are included where data on host snails are lacking. Infection by larval Trematoda, including *Schistosoma*, can influence functions such as growth, fecundity and the ability to aestivate successfully and so modify the effects of abiotic environmental factors. These effects of trematode infection have been reviewed by Wright (1966) and are not considered here.

The joint OIHP/WHO Study Group on Bilharziasis, which met in Cairo in 1949, recommended the collation by World Health Organization consultants of accurate records of the geographical distribution of bilharziasis and its snail intermediate hosts. These consultants presented their findings at the WHO African Conference of Bilharziasis in Brazzaville (November 26-December 8, 1956). This contributed much to the knowledge of the world-wide endemicity of the disease and to the identification of the intermediate host snail species involved, culminating in the monograph on the taxonomy of these snails by Mandahl-Barth (1957a,b). At an earlier meeting (3-9 October of the same year) in Paris, however, the WHO Study Group on the Ecology of Intermediate Snail Hosts of Bilharziasis stressed that without a knowledge of the relationships between the ecology of host snail habitats, snail life cycles and habits, practical control measures would have only limited success. Although isolated ecologically oriented studies had been made earlier (Gordon et al., 1934; Barlow, 1935; Mozley, 1939; Barlow & Muench, 1947), the proceedings of this Paris conference, published in 1958 in Vol. 18 (pts. 5-6) of the *Bulletin of the World Health Organization*, and Mandahl-Barth's earlier monograph laid the foundation for further research into the ecology of the disease.

Between 1950 and about 1964, then, medical malacologists were concerned primarily with field ecological survey studies. Abiotic factors which were thought likely to influence host snail distribution were examined in various countries in a generalized way, often incorporated into composite studies. These factors included analyses of water chemistry, observations on temperature, sunlight, turbidity, current velocity, dessication and substratum. Most attention

---

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has, however, been given to 3 of these, chemistry, temperature and dessication and their influences on the snails' life cycles.

Where authors have referred to *Taphius glabratus* Say or *Australorbis glabratus* (Say) and *T. centrimetralis* Lutz or *A. centrimetralis* (Lutz), these are replaced in the discussion below by the currently accepted names *Biomphalaria glabrata* (Say) and *Bi. straminea* (Dunker), respectively.

WATER CHEMISTRY

General chemical analyses of water from snail habitats have been described by a variety of authors in many countries (Alves, 1958 in Rhodesia; Azevedo et al., 1961 in Mozambique; Meillon et al., 1958 and Schutte & Frank, 1964 in South Africa; El Gindy, 1957 and Gohar & El Gindy, 1960b in Egypt; Andrade, 1954 and Andrade et al., 1955 in Brazil; Harry et al., 1957 and Harry & Aldrich, 1958 in Puerto Rico; Lietar, 1956 in what is now Zaire; Marill, 1958 in Algeria; Mozley, 1939 and Webbe, 1962a in what is now Tanzania; Teesdale, 1962 in Kenya and Watson, 1958 in Iraq). These and other more generalized studies (Deschiens, 1957b; WHO, 1957; Hubendick, 1958) demonstrated that host snails are tolerant of waters differing widely in chemical content so that their occurrence seems independent of the usual range of ionic composition found in field waters. Levels of salts lethal to snails are obviously seldom approached here and snails may even be expected to survive anoxic conditions (Alberts, 1966). Variation in population density may, however, be attributable to the chemical quality of water, and subsequent work has centered around more specific aspects of the chemical regime.

The salt calcium bicarbonate was thought to have effects, though perhaps only subtle ones, on host snail physiology. This is really the only aspect of water chemistry where effects on host snail ecology have been investigated in depth, chiefly by Rhodesian and South African researchers. The concentration of the bicarbonate anion (alkalinity) is an indication of the buffering capacity of the water and since much of the snails' endemic waters in southern Africa flow over the insoluble Old Granite and Gneiss formations of the Archaean Complex, its effect on snails might provide information applicable over a large area. Boycott (1936) and Macan (1949, 1950) had found that pulmonate snails in Britain had threshold calcium concentrations below which they could not survive. Critical values for *Lymnaea (Radix) peregrer* (Müller) and *Planorbis albus* (Müller) in the English Lake District lay at 3 and 5 mg/l Ca^{++} respectively (Macan, 1949).

Harrison et al. (1966) showed that egg production by *Biomphalaria pfeifferi* (Krauss) kept in both natural stream water and artificial culture medium with high magnesium/calcium ratios (12.4 and 19.7 respectively) was significantly impaired and even prevented when compared with controls in which the cations were in equal proportions. Such magnesium-rich water flows off the soluble rocks of the Swaziland System which is associated with the Great Dyke in Rhodesia. Host snails are absent from these rocks (Shiff, pers. comm., 1975), which are largely serpentines (hydrous magnesium silicates). In the Republic of South Africa, the Swaziland System is more widespread, and similar magnesium-rich water is characteristic of parts of the Kaap and eastern Crocodile River systems in the southeastern Transvaal. Although host snails are also rare on these rocks, Schutte & Frank (1964) did not find the water flowing off these formations (with mean Mg/Ca ratios of up to 17.4, based on monthly analyses) to be unfavourable to their presence.

Frank (1963) and Schutte & Frank (1964) also pointed out that the sodium/calcium ratio may affect snail density and that *Bulinus (Physopsis)* was more common than *Biomphalaria pfeifferi* in waters where the ratio exceeded 2.4. They referred to observations by Malek (1958) that a low ratio was unfavourable for snails, only *Bi. pfeifferi* being found where the value was 0.2.

Frank (1963), Schutte & Frank (1964) and Williams (1970a) have shown that while *Bulinus (Physopsis)* sp., *Bu. (P.) globosus* (Morelet) and *Biomphalaria pfeifferi* occur in waters with calcium bicarbonate concentrations ranging from 5-40 mg/l Ca^{++} and 20-200 mg/l HCO_3^- (very soft to very hard), they are most abundant in the hardest waters, above approximately 30 mg/l Ca^{++} and 200 mg/l HCO_3^-. In Rhodesia, *Bi. pfeifferi* was absent from very soft waters (<5 mg/l Ca^{++} and <20 mg/l HCO_3^-). In South Africa, the frequency of host snail occurrence was found to be more or less proportional to water hardness, hard and very hard waters being favoured. The hardness of these latter waters was frequently due not to calcium, as Schutte & Frank (1964, Fig. 5) might suggest, but to magnesium, which is plentiful in the serpentines and magnesite ($MgCO_3$) of the Swaziland and Moodies Systems. A high magnesium content is, as mentioned above, typical of the watercourses draining these rocks. Calcium-bearing rocks are rare in this area.

The findings of Williams (1970a,b), using the intrinsic rate of natural increase (r), also demonstrated that *Bulinus (Physopsis) globosus* is tolerant of a wider range of calcium and bicarbonate ion concentrations than *Biomphalaria pfeifferi*. Williams found *Bi. pfeifferi* to exhibit greater variation in 'r' at different concentrations under experimental conditions than *Bu. (P.) globosus*, with peak values within the 'medium' category (5-40 mg/l Ca^{++} and 20-200 mg/l HCO_3^-). Further, the field abundance of *Bi. pfeifferi* was significantly correlated with 'r' ($p<0.05>0.025$), whereas for *Bu. (P.) globosus* this was not so.

Harrison & Shiff (1966) and Harrison et al. (1970) criticized Williams' experiments on the grounds that his snails had done best in the water from which they had been collected (the only natural water used). They therefore repeated the experiments using snails from widely separated habitats and water of differing $CaCO_3$ content. Their results confirmed the attainment of the highest 'r' in 'medium' water as reported by Williams, but showed as well that snails from geographically distinct populations differed both in their age at first oviposition and in egg output. Harrison (1966) commented that because these populations had been separated at least since early Pleistocene times, genetically isolated populations or perhaps strains could now exist, each with its own physiological characteristics. He has, in addition, (Harrison, 1968) endorsed the finding that bicarbonate ion concentrations within the 'medium' range of Williams (1970a,b) are most suitable for host snails by demonstrating that oxygen consumption by *Biomphalaria pfeifferi* varied significantly at different HCO_3^- levels, from 15-300 mg/l (as $CaCO_3$). He found that the highest oxygen uptake rate occurred at a bicarbonate concentration of 35 mg/l, falling off rapidly above and below this level.

Jennings et al. (1973), employing electrical conductivity as a measure of total dissolved solids (TDS), have shown that for *Biomphalaria pfeifferi* 'r' varied markedly under conditions of differing conductivity. Tested over a range of 50-1000 μS, the species attained highest 'r' values between 300 and 400 μS, the conductivity range associated with hard water by Schutte & Frank (1964). Jennings et al., however, changed the experimental temperature from 26° to 29°C once the snails had reached maturity and since, as will be mentioned later, 'r' varies with temperature, this might have affected the very high 'r' values recorded (up to 1.15). Heeg (1975) has shown that the occurrence of *Bulinus (Physopsis) africanus* (Krauss) in waters with widely different dissolved solid content may be explained by the snail's ability to acclimate to changes in TDS of the magnitude expected in natural waters. *Biomphalaria pfeifferi*, which is known to be particularly sensitive to the ionic composition of water (Frank, 1963; Harrison, 1966, 1968; Williams, 1970a,b; Jennings et al., 1973), may not have this ability. This could account, to some extent at least, for its irregular and more restricted distribution pattern in southern Africa.

These findings indicate that while water quality within the usual ranges found in natural habitats may not affect the snails' distribution pattern much, certain aspects may influence their local abundance. The findings show further that *Bulinus (Physopsis)* has a greater tolerance to changing chemical conditions, both in the field and in the laboratory, than does *Biomphalaria pfeifferi*, whose population density may be determined at least partly by

factors such as the Ca^{++} and HCO_3^- concentrations.

SALINITY

Although references to bilharzia transmission in lagoons and estuaries are to be found in the literature (Blair, 1956; Malek, 1958; Watson, 1958; Gilles et al., 1965), little information is available on the effects of saline water on the host snails. Brumpt (1941) showed that *Biomphalaria glabrata* could survive for 35 days in sea water of 2 °/oo and for only a few days at 2.5 °/oo. Chernin & Bower (1971) found that the same species could survive in artificial sea water at or below a concentration of 1.25 °/oo. Ezzat (1961) reported that Egyptian *Lymnaea (Radix) natalensis* Krauss was intolerant of saline water and lived for only 48 hours in water of 3 °/oo. It seems, therefore, that even very low salinities are inimical to the snails, but since claims are made from time to time that bilharzia transmission does occur in Natal estuaries, attention should be paid to the snails' tolerance of fluctuating salinities, i.e., tidal conditions. Bruton & Appleton (1975) did, in fact, find a freshwater snail, *Melanoides tuberculata* (Müller), living under just such conditions in the Mgobezeleni estuary in northern Zululand.

TURBIDITY

Although host snails are frequently found in naturally turbid waters, those with high turbidities (due mainly to minerals in suspension) are considered unfavourable (Malek, 1958; Watson, 1958). Experiments by El Gindy (1957) revealed turbid Nile flood water to have no appreciable effects on either *Bulinus (Isidora) truncatus* (Audouin) or *Biomphalaria alexandrina* (Ehrenberg). Recently Harrison & Farina (1965) have shown that while a turbidity of 360 mg/l (due to suspended minerals from granite erosion) did not affect snails themselves, it prevented development and hatching of *Bi. pfeifferi* eggs. Neither *Bu. (Physopsis) globosus* nor *Lymnaea natalensis* were similarly affected at this concentration and eggs of all 3 species hatched normally at a lower level of 190 mg/l.

In the eastern Transvaal lowveld, Schutte & Frank (1964) found that turbidity, which is highest in summer, occasionally exceeded 150 mg/l. It was due mostly to fine siliceous and clayish matter and was highest in soft waters where the snails were least common anyhow.

TEMPERATURE

Observations based largely on isolated recordings have shown that host snails have broad tolerance ranges to field water temperatures (Gordon et al., 1934; van Someren, 1946; Zakaria, 1955; Ayad, 1956; WHO, 1957; Malek, 1958; Watson, 1958). These temperatures vary from zero to around 40°C, although this seasonal range depends upon the climate of the region concerned. The favourable range lies between approximately 18° and 32°C, with optimal conditions between 22° and 26°C. Diurnal ranges of up to 20°C have been recorded from habitats containing *Biomphalaria pfeifferi* on the Kenyan highlands (van Someren, 1946). However, these remarkably broad tolerances may not be accurate since, as Shiff (1966) has demonstrated both experimentally and in the field, *Bulinus (Physopsis) globosus* is sensitive to temperature gradients and will seek out parts of the habitat where temperatures are nearest the optimum (i.e., the surface layers during the cool Rhodesian highveld winter). It would be interesting to know whether *Bi. pfeifferi* exhibits a similar behaviour pattern. Macan (1961) has emphasized that temperature tolerance ranges should be viewed as an optimum zone merging into one of unfavourably high and one of unfavourably low temperature. Distribution is limited by temperature mainly where this becomes unfavourable for reproduction.

Laboratory investigations have shown that although the temperatures at which host snails attained an optimal 'r' were similar, the range at which 'r' remained high varied for different species, just as tolerances to $CaCO_3$ concentrations do. Shiff (1964a) worked on Rhodesian *Bulinus (Physopsis) globosus;* Sevilla (1965) on 3 species of *Biomphalaria*, Tanzanian *Bi. pfeifferi*, Egyptian *Bi. alexandrina* and Puerto Rican *Bi. glabrata;* Sturrock (1966) on Tanzanian *Bi. pfeifferi;* Shiff & Garnett (1967) on Rhodesian *Bi. pfeifferi* and Sturrock & Sturrock (1972) on St. Lucian *Bi. glabrata*. The highest 'r' value for each of these species was found to occur at 25°C. Values for *Bu. (P.) globosus* rose to a distinct peak at 25°C (Shiff, 1964a), whereas for *Bi. pfeifferi* Shiff & Garnett (1967) found a plateau of optimal though lower 'r' values between 20° and 27°C. Shiff & Husting (1966) considered this to indicate that *Bu. (P.) globosus* is profoundly influenced by temperature and that it can multiply rapidly under optimal conditions, even if these are of brief duration. *Biomphalaria pfeifferi*, however, showed little change in 'r' over a 7°C range of experimental temperatures, none producing a marked peak in 'r', which suggests an adaption to stable thermal conditions. The high values of 'r' attained by *Bu. (P.) globosus* at 25°C and 27°C (0.66 and 0.60 respectively) may, therefore, be considered a selective advantage to the species, enabling it to take advantage of the harsh environmental conditions found in temporary bodies of water on, for instance, the highveld plateau of central and southern Africa. In the absence of a clear 'r', *Bi. pfeifferi* may be expected to colonize more permanent habitats with cooler temperature regimes and this is precisely the type of habitat harbouring the species in southern Africa. Hira (1975) has in fact drawn attention to the permanence of host snail habitats, noting that on the Zambian plateau *Bulinus (Physopsis)* occurred principally in temporary bodies of water, whereas *Bi. pfeifferi* was found mostly in perennial streams and impoundments.

Tanzanian *Biomphalaria pfeifferi*, Egyptian *Bi. alexandrina* and Puerto Rican *Bi. glabrata* (Sevilla, 1965) and St. Lucian *Bi. glabrata* (Sturrock & Sturrock, 1972) showed no evidence of a plateau of 'r' values, but rather peaks at 25°C similar to *Bulinus (Physopsis) globosus* (Shiff, 1964a). Sturrock (1966) used only 3 experimental temperatures, so that although there appears to be a peak at 25°C, the existence of a plateau cannot be excluded. All these species are known to be inhabitants of temporary bodies of water. The genus *Biomphalaria* in the southern part of its range in Africa thus appears to be adapted to permanent habitats, whereas further north and in the New World its high intrinsic rate of natural increase at high temperatures enables it to survive in habitats which dry out regularly. High rates of increase involve high energy output, which would be facilitated by natural selection in populations that are decimated periodically (Hairston, 1973).

Prinsloo & van Eeden (1969) have shown another South African planorbid (although not a vector of human bilharziasis), *Bulinus (Isidora) tropicus* (Krauss), to have its highest 'r' at the highest temperature tested (27°C). This rate fell with decreasing temperature. A repeat of these experiments using temperatures above 27°C might have produced a more satisfactory result. They also found that *Lymnaea (Radix) natalensis* had a peak 'r' at 18°C. Using data from the same experiments, Prinsloo & van Eeden (1973) have illustrated the differences in growth rates (measured as weight increases) of *Bu. (I.) tropicus* and *L. (R.) natalensis* recorded at constant temperatures from 15° to 27°C. The authors' (1969) contention was "that a statistically significant correlation between the country-wide distribution patterns of *L. natalensis* and *Bulinus (Physopsis)* sp. (van Eeden & Combrinck, 1966) might reflect common ecological requirements" and could therefore allow findings for the former to be applied to the latter. This hypothesis must be questioned, however, because not only do the findings of Prinsloo & van Eeden (1969) "militate against the occurrence of both species in Natal and the Transvaal lowveld" (where, in fact, they are abundant), but also because *L. (R.) natalensis* has been shown to undergo a fundamentally different life cycle to that of *Bu. (P.) globosus*. The former breeds during the cooler months, which may explain the low

optimal temperature of 18°C, whereas the latter breeds during the warmer months (Appleton, 1974). Differences in their ecological requirements are further indicated by the much greater susceptibility of *L. natalensis* to dessication than *Bu. (P.) globosus* (Shiff, 1960; Cridland, 1967) and the evidence provided by Calow (1970, 1973, 1974) on *L. (R.) peregrer* and *Planorbis contortus* (Linnaeus) suggesting that Lymnaeidae are herbivores whereas Planorbidae are detritivores.

Kock (1973) determined 'r' at different temperatures for 5 South African pulmonate species. He concluded that for the 3 Bulininae investigated peak values lay between 23° and 26°C for *Bulinus (Physopsis) africanus* between 26° and 28°C for *Bu. (P.) globosus* and at 26°C for *Bu. (Isidora) tropicus. Biomphalaria pfeifferi* and *Lymnaea (Radix) natalensis* had plateaus of near-optimal 'r' values, from 26° to 29°C and 23° to 26°C respectively. These temperatures are noticeably higher, some by several degrees, than those calculated for *Bu. (P.) globosus* and *Bi. pfeifferi* by other authors (Shiff, 1964a; Sevilla, 1965; Sturrock, 1966; Shiff & Garnett, 1967) and for *L. (R.) natalensis* by Prinsloo & van Eeden (1969), although their findings for *Bu. (I.) tropicus* are similar. The existence of a plateau of near-optimal 'r' values for *Bi. pfeifferi* does, however, agree with the results of Shiff & Garnett (1967). Kock attributed his remarkably high optimal temperatures, especially for *Bi. pfeifferi*, to the parental generations of his experimental snails being native to hotter areas than those used by other authors (his *Bi. pfeifferi* came from Plaston near Nelspruit in the eastern Transvaal).

The difference found by Kock between *Bulinus (Physopsis) africanus* and *Bu. (P.) globosus* is interesting and suggests that the former is adapted to cooler conditions than the latter. This is supported by the findings of Brown (1966, 1967), who showed that in Natal and the southeastern Transvaal *Bu. (P.) globosus* is confined to the lowlands, while *Bu. (P.) africanus* extended inland onto the Transvaal highveld and southwards into the Transkei. Schutte & Frank (1964) found the 2 species to be sympatric on the eastern Transvaal escarpment.

Populations of planorbid host snails expand optimally at constant temperatures around 25°C. Those species which have a distinct peak 'r' (usually 0.7-0.9) are capable of successful aestivation over prolonged periods of drought and thrive under naturally unstable or temporary conditions. Those with lower maximal 'r' values (0.4-0.5) spread over a range of temperatures, however, inhabit more stable environments and do not aestivate readily. Host snail distribution patterns in southern Africa are thus determined more by the permanence of available habitats than by temperature differences between them.

Intrinsic rates of natural increase under field conditions have been calculated for a few snail species. Dazo et al. (1966) reported values of 0.61 and 0.67 for Egyptian *Biomphalaria alexandrina* and *Bulinus (Isidora) truncatus* respectively. These values are lower than the maxima given by laboratory experiments, but this is to be expected in view of the added environmental pressures, such as fluctuating temperatures, predation and infection by larval Trematoda, which must affect 'r'. Sturrock (1973a) went further and demonstrated that in a variety of shallow habitats (4 different types) on St. Lucia mean 'r' values for *Bi. glabrata* varied from 0.45 during the increasing phase of population growth to -0.08 during the stable phase, and to -0.75 during the decreasing phase. Unfortunately, he did not make it clear whether all or only some of these sites were temporary. Under permanent conditions one might expect the decline of the decreasing phase to be less drastic.

An important contribution to the *modus operandi* of the effect of temperature on 'r' is provided by van der Schalie & Berry (1973), who investigated temperature effects on growth and reproduction in members of 3 North American pulmonate families and one prosobranch family. They found that although the optimum temperatures for 3 species of *Helisoma*, i.e., *H. trivolvis* (Say), *H. anceps* (Menke) and *H. campanulatum* (Say) (Pulmonata: Planorbidae) differed slightly, they fell within the 24°-26°C range. At higher temperatures, growth was

better, but it was offset by poor egg production, which dropped close to zero at 30°C. Optima for 2 Lymnaeidae (Pulmonata), *Lymnaea (Lymnaea) stagnalis* Linnaeus and *L. (Stagnicola) emarginata* Say, lay at approximately 22°C, while *Physa gyrina* Say (Pulmonata: Physidae) had a wider tolerance range altogether (14° to 24°C). The only prosobranch tested, *Amnicola limosa* (Say) (Prosobranchia: Amnicolidae), was found to perform optimally in the 18° to 24°C range. Histological examination of gonads showed that at temperatures above and below the optimum range, tissue development was impaired. Little or no gonad activity was evident at sub-optimal temperatures, although above the optimal range egg and sperm differentiation seemed in some cases to be normal. At these higher temperatures, however, fewer eggs were laid and their viability fell to about 50% of that within the optimal range. These results support those of Michelson (1961), who found an optimum temperature of 25°C for *Biomphalaria glabrata*, and that at 30°C, although growth was accelerated, repression of the female gonadial tissues occurred. Temperatures below the optimum retarded both growth and reproductive activity.

A recent field study on the coastal peneplain of southeastern Africa (Appleton, 1976a) has revealed a partial correlation (significant at the 1% level) between increasingly high thermal regimes and reduced fecundity in *Biomphalaria pfeifferi*. By expressing these regimes as a variety of components, it was possible to isolate one, the number of degree hours >27°C per week during spring and early summer (the maturation period of the *Bi. pfeifferi* 1st generation of Appleton, 1974), as that which influenced fecundity most. The critical level during this period lay between 120-179 deg. h. >27°C/wk., and the species was absent from habitats which exceeded this limit. This provides an explanation for the discontinuous distribution of *Bi. pfeifferi* on this peneplain.

Though there is a lack of continuous temperature data from temporary habitats, particularly during the actual drying process, temperature is clearly an important limiting factor to host snails in lentic environments, chiefly through its influence on fecundity. Although both the upper and lower critical limits lie at temperature levels commonly encountered in the field, its influence in river systems appears to be subordinate to that of current velocity (Appleton, 1976b).

The more dynamic aspects of thermal regimes may also be important. Daily warming and cooling rates have been held to provide the stimuli responsible for the observed nocturnal activity patterns of several terrestrial and aquatic Pulmonata (Dainton, 1954a,b; Karlin, 1961; DeWitt, 1967; Hunter, 1968).

POPULATION FLUCTUATIONS

Numerous observations of fluctuations in the abundance of host snails have been reported. Reviewing the evidence, Webbe (1964) and Webbe & Jordan (1966) stressed the apparent dependance of reproductive and population cycles on the cyclic fluctuations of interrelated environmental factors. Generally, the evidence shows a fall in snail densities during rainy periods, with little or no breeding. During the ensuing drier and warmer months, however, reproductive activity increases. Populations appear to follow an average growth curve, of which the maxima and minima are related to rainfall and temperature or environmental conditions due to them (Webbe, 1962a; Sturrock, 1973a). In another review, Hairston (1973) noted that in sub-tropical and temperate regions population fluctuations were attributed largely to temperature influences while those in tropical areas were thought due to rainfall. An alternative approach is adopted here. Since fecundity and survival are influenced by drastic alterations of the habitat – periods of physical stress – the permanence of habitats involved is taken into account and reduces the apparent lack of concensus among these reports.

Habitats in which host snail life cycles have been investigated fall into 2 broad categories – temporary and perennial or permanent (the same criteria used by Mandahl-Barth, 1954; Cridland, 1957a,b, 1958; and Hira, 1975). Temporary habitats dry up for part of each year and include irrigation canals which may, like those in Egypt, be emptied annually for cleaning. As Mandahl-Barth (1954) has pointed out, these two habitat types place different demands on snails, particularly on their ability to withstand dessication. Only species capable of surviving through the dry season will survive in temporary habitats. This ability has since been demonstrated to be coupled with a peak 'r' value at high temperatures. It enables populations which survive periods of physical stress and heavy mortality to reproduce rapidly when conditions again permit, as recorded in the field by Pringle & Msangi (1961) and McCullough (1962). Phenomena which should be regarded as periods of stress are drying of the habitat and prolonged high and low temperatures, these latter affecting fecundity and possibly survival as well. In temporary habitats influences such as these must determine the snails' life cycles. Floods may sometimes be important. Pimentel & White (1959) and Rowan (1959) found in Puerto Rico that only the most severe floods caused serious reductions in the densities of *Biomphalaria glabrata* populations in streams there. Molluscicide applications might also fall into this category.

In temporary habitats in tropical South America and the West Indies, *Biomphalaria glabrata* in Brazil and St. Lucia and *Bi. straminea* in Brazil have a single generation per year (Olivier, 1955; Olivier & Barbosa, 1955a,b; Barbosa, 1962; Andrade, 1962b; Jobin, 1970 and Sturrock, 1973b). At the close of the rainy season snails are numerous and most are large but when the habitats dry out many snails die and relatively few aestivate successfully. With the onset of the next rainy season these survivors, mostly smaller specimens, grow and reproduce rapidly. Within 50-60 days peak snail abundance has been restored. The snails seldom live beyond a year.

In an important quantitative contribution, Shiff (1964b) examined the life cycle of *Bulinus (Physopsis) globosus* in a temporary pond in Rhodesia. He found a cycle of 1 generation per year clearly related to both rainfall and temperature. By calculating seasonal rates of increase, he demonstrated that when temperatures were high (summer) fecundity was also high although longevity was reduced. The small proportion of snails attaining maturity were able to regenerate the population. When temperatures were low (winter), fecundity was reduced but offset by increased longevity. The species is therefore equipped to survive in both large bodies of water where moderate temperatures permit moderate fecundity with increased longevity and in small, temporary habitats where environmental conditions are severe, by responding to brief optimal spells with high egg production. The resultant massive increase in numbers ensures the survival of the population during adverse conditions, despite poor longevity. This cycle was confirmed by Hira & Muller (1966) in a temporary habitat in Nigeria.

In the Middle East and North Africa where many habitats are temporary, the rainy season extends from December to April (winter). However, in Iraq, Watson (1951, 1958) found that *Bulinus (Isidora) truncatus* underwent 2 generations per year in the field. Numbers increased during early summer (May and June) after the emergence of individuals aestivating through the cold winter and/or winter closure of irrigation canals, reaching peak abundance in July with a smaller 2nd peak in autumn (October) after the maximal summer heat. Temperatures here frequently approach 39° to 40°C (Pitchford, pers. comm., 1975). Pronounced reproductive activity in June and September accounted for the 2 peaks. This pattern was also confirmed in Iraq by Najarian (1961); by Dazo et al. (1966) and Mousa & El Hassan (1970, 1972) in Egypt; by Marill (1956, 1958) in Algeria and by Gaud & Dupuy (1954) and Gaud (1958) in Morocco. Dazo et al. (1966) also showed that *Biomphalaria alexandrina* had a similar life cycle. In these regions both the drying of the habitats and the extremely high summer and low winter temperatures may be considered to be periods of stress and were followed by intense egg laying.

In tropical Africa many host snail habitats are also temporary, but there are 2 usually distinct rainy periods each year: the 'long' rains from April to May and the 'short' rains from November to December. These are due mainly to the southeast and northeast monsoon winds. A belt of 'rain in all seasons' lies along the equator, extending approximately 7-8° to the north and south.

Studies by Mozley (1939), Webbe & Msangi (1958), Webbe (1962a) and Sturrock (1965) in what is now Tanzania; Cridland (1957b, 1958) in Uganda; Teesdale (1962) in Kenya; Lietar (1956) in what is now Zaire and Odei (1967) in Ghana associated observed population fluctuations by various snails of the genera *Bulinus (Physopsis)* and *Biomphalaria* with the change from dry to wet conditions. Two generations per year were usual. Increased egg laying was apparent following the advent of each rainy period, so that both appear to consitute periods of stress. The number of generations produced each year depends, however, on the permanence of the habitats during the period between the 'long' and 'short' rains (January-March).

In permanent habitats, the effects of rainy periods are not as profound as in temporary ones and temperature regimes are more stable. Studies in such habitats have revealed that egg production occurs throughout the year, with a major breeding season in spring and summer, and not in 1 or 2 isolated bursts, as in temporary bodies of water. Andrade (1962 a,b) and Ritchie et al. (1962) found that *Biomphalaria glabrata* in permanent streams in Brazil and Puerto Rico, respectively, produced single density peaks at the start of each rainy season. Cridland (1957a) and Webbe (1960, 1962b) found only a single peak per year for *Bi. adowensis* (Bourguignat), *Bi. sudanica* (von Martens) and *Bi. pfeifferi*. Populations declined markedly following the 'long' rains, but were unaffected by the 'short' rains. The stability of the 2 habitats in question, a permanent pond in Uganda and Lake Duluti in Tanzania, may account for the observed mild effects of the 'short' rains. Malek (1962) reported a similar cycle for *Bulinus (Isidora) truncatus* in the Sudan, as did Berrie (1964) for *Bu. (Ph.) ugandae* (Mandahl-Barth) and *Bi. sudanica* in a permanent habitat in Uganda; Baalawy & Moyo (1970) for *Bu. (P.) nasutus* (von Martens) in Tanzania and Onambiro (1972) for *Bu. (P.) globosus* in Sierra Leone.

Contributions by McCullough (1957) on permanent habitats in Ghana and Appleton (1974) on South Africa, regions with only 1 rainy period per year, revealed an annual cycle of 3 overlapping generations for *Bulinus (Physopsis) globosus* and *Biomphalaria pfeifferi*. McCullough found that peaks occurred simultaneously in the 4 habitats he sampled, in December-January, March-June and September-October. Further studies on *Bu. (Isidora) truncatus rohlfsi* (McCullough, 1962) confirmed this. The pattern found by Appleton was similar, and although the specific identify of the *Bulinus (Physopsis)* was not given, D. S. Brown has since examined examples from several localities on the stream concerned and found only *Bu. (P.) globosus* (Brown, pers. comm., 1975). The snails sampled by Appleton therefore appear to be a homogeneous *Bu. (P.) globosus* population. Hira (1975) identified 2 breeding periods per year for *Bi. pfeifferi* in Zambia. His fortnightly samples are, however, reduced to mean monthly densities, which could obscure the more subtle fluctuations.

The study by Appleton (1974) revealed density peaks due to new generations in early and late summer (1st and 2nd generations respectively) and late autumn (3rd generation). These were sometimes small in size and probably not recognizeable as such when, as in many of the studies referred to above, snail sizes were not considered, densities were categorized (rare, common or abundant) and between-sample intervals were long (monthly or even six-weekly). When expressed as snail density (number of snails per sample) and not subdivided into size classes, the data of Appleton (1974) presents a pattern with 1 major peak from October to December (1st generation) and minor peaks in February (2nd generation) and May (3rd generation). This presentation corresponds to those of other authors and the 3 generation per year cycle is thought to be a more accurate picture of the sequence of events in permanent bodies of water.

Some variation in life cycles in different geographical areas may be normal, however. Berrie (1965) recorded a biennial cycle for *Lymnaea (Lymnaea) stagnalis* in a marginal habitat, whereas this was condensed into an annual one under more favourable climatic conditions. Temperature was suggested as a possible controlling factor here.

CURRENT VELOCITY

Host snails have been found to have a remarkably narrow tolerance range to current velocity. Most habitats in which they occur are lentic; but established, persistent populations occur also in very slowly flowing water, up to a limit of approximately 0.3 m/sec. (Luttermoser, 1944; Zakaria, 1955; Pimentel & White, 1957; Witenberg & Saliternik, 1957; WHO, 1957; Watson, 1957, 1958; Meillon et al., 1958; Frank, 1964; Jobin & Ippen, 1964; Etges & Frick, 1966; Appleton, 1975). Scorza et al. (1961), however, provided a convincing illustration of this by showing a nearly linear negative correlation between the density of *Biomphalaria glabrata* and current velocity, with a limit at 0.25-0.30 m/sec. in a stream in Venezuela. Only *Bi. glabrata* has so far been reported able to actively migrate upstream against weak currents. Radke & Ritchie (1961) described this as a common phenomenon in slowly flowing streams in Puerto Rico and Paulini (1963) found the same species capable of migrating against a velocity of 0.1 m/sec. in Brazil. The observation by Wright (1971) that the scarcity of host snails in the third of Africa with a mean annual rainfall of over 150 cm (i.e., the Congo River basin and coastal areas bordering the Gulf of Guinea) may be due to the characteristically rapid flow of streams there, and suggests that rainfall patterns are also relevant.

The reason for such a definite critical limit at 0.3 m/sec. may be that the snails simply cannot remain clinging to a substratum exposed to greater velocities for any length of time. Jobin & Ippen (1964) have shown that the hydrodynamic drag force created by velocities between 0.20 and 0.33 m/sec. at shell height caused *Biomphalaria glabrata* to become immobilized on solid canal surfaces. At velocities greater than 0.33 m/sec. the snails became dislodged and swept away.

This dislodging of snails has been the favoured *modus operandi*, but a limiting of the availability of preferred food may also be important. Recently Calow (1973, 1974) has shown the European planorbid *Planorbis contortus* to be a detritus feeder, particularly when the detritus is infected with live bacteria. This supports the contention of Boettger (1944) that the Planorbidae generally are detritivores, and casual observations by Oliff (1953), Malek (1958), Watson (1958) and Stiglingh & van Eeden (1970) that planorbids show a partiality for decaying matter, both animal and vegetable. Detritus will only be deposited, however, under lentic or very slowly flowing conditions, probably being carried away at velocitites above 0.3 m/sec.

The rate of host snail dispersal via passive drift has never been measured. Boray (1963), however, reported a rate of 20-300 *Lymnaea (Austropeplea) tomentosa* (Pfeiffer) per week from a dam with an average snail density of 96/m^2 in Australia.

WAVE ACTION

Watson (1957) noted that severe wave action, particularly on steeply shelving shores, was inimical to *Bulinus (Isidora) truncatus*. This factor, which may be expected in large bodies of water, is difficult to measure accurately, although useful comparisons of exposed conditions can be made (Field, 1968). Recent observations in Lake Sibaya (northeastern Natal) by the present author suggest that *Bu. (Physopsis) globosus* is more tolerant of wave action

than *Biomphalaria pfeifferi* and may commonly be exposed to waves up to at least 10 cm high for prolonged periods. Measurements with an Ott current meter showed the mean velocity over 5 minute periods to be 0.16 m/sec., although that of wave surges albeit brief was obviously very much greater. Emergent reed beds reduce wave action considerably and their role in the distribution of host snails in lakes is worthy of investigation.

WATER DEPTH AND HYDROSTATIC PRESSURE

Hydrostatic pressure increases by approximately 1 atm. (1.01×10^4 Pa) for every added 10 m water depth. Although increased pressure will decrease buoyancy, presumably by affecting the air bubble in the mantle cavity, it does not seem a significant factor in the usual host snail habitats. These snails are generally found in shallow water near the margins of their habitats and rarely below 1.5-2.0 m (WHO, 1957), although isolated records show them capable of living in deeper water, mostly in lakes. Veloso (1955) found *Biomphalaria glabrata* down to 3 m in muddy water in Brazil and Mandahl-Barth (1954) recorded *Bi. smithi* Preston from 4.3 m in Lake Edward and *Bi. choanomphala* (von Martens) from 12.2 m in Lake Victoria. He considered this last species to be a predominantly lacustrine one. Appleton (1976a) recorded *Bi. pfeifferi* down to 4.5 m in sheltered, submerged weed beds in Lake Sibaya.

Various bulinids of the subgenus *Bulinus (Isidora)* are known from considerable depths in lakes. *Bu. (I.) trigonus* (von Martens) is recorded by Mandahl-Barth (1954) from 7.3-9.2 m in Lake Victoria; Gillet et al. (1960) found *Bu. (I.) coulboisi* (Bourguignat) at 2.7 m in Lake Kivu and Wright et al. (1967) dredged *Bu. (I.) nyassanus* (Smith) from 2-16 m and collected *Bu. (I.) succinoides* (Smith) from 3-4 m, in Lake Malawi. Bruton (unpubl. data, 1971) recorded *Bu. (I.) natalensis* (Küster) down to 9 m in Lake Sibaya. No members of the subgenus *Bulinus (Physopsis)* appear to have been found beyond about 2 m in depth.

Experiments by Deschiens & Jardin (1954) with *Biomphalaria adowensis* and *Bi. glabrata* and by Gillet et al. (1960) using *Bi. pfeifferi* showed these species capable of surviving at depths down to 10-15 m for periods of up to 6 weeks. However, the small scale of these experiments (especially the former) and the lack of replication render these findings inconclusive. No comparable trials with bulinids appear to have been done, although Alberts (1966) has suggested that, given aerobic conditions and favourable temperatures, *Bulinus (Physopsis) africanus, Bu. (Isidora) tropicus* and *Lymnaea natalensis* can survive well for several days at least, without access to an air/water interface, using cutaneous respiration alone.

Seasonal migrations from shallow to deeper water as temperatures fall and in the reverse direction as temperatures rise have been described by Cheatum (1934) for various Pulmonata in a palearctic lake and supported by Clampitt (1972) with respect to *Physa integra* Haldeman, but not *Helisoma antrosa* (Say). No comparable information is available for lacustrine populations of host snails.

Pressure becomes relevant in irrigation systems pumping water from host snail habitats and may usefully be included here. Pitchford (1953) found that pressures of 6.47-10.21 atm. (65.49×10^4-103.4×10^3 Pa) for 10-15 minutes (far in excess of that normally built up by centrifugal pumps) had no observable effect on juvenile *Bulinus (Physopsis)* sp., *Biomphalaria pfeifferi* and *Lymnaea (Radix) natalensis*. Snail eggs withstood pressures of 6.81-8.51 atm. (68.96×10^4-86.18×10^4 Pa). Therefore, centrifugal pumps do not eliminate snails. Ram pumps do, however, appear to prevent the passage of snails, which are presumably crushed by the valves, although theoretically they could escape by being carried through on the upstroke.

DESSICATION

While host snail populations are able to persist in temporary habitats through the ability of a portion of their number to aestivate successfully during periods of drought, species and strains differ in their resistance to dessication (WHO, 1957). Barlow (1933, 1935) demonstrated that members of the genera *Bulinus* and *Biomphalaria* could survive the winter closure of Egyptian irrigation canals (a drying period of 40-50 days), and that they laid eggs immediately after refilling. Cawston (1946) noted the resistance of *Bu. (Physopsis) africanus* to environmental influences during droughts in South Africa, and Annecke & Peacock (1951) found large numbers of *Bu. (Isidora) tropicus* aestivating amongst grass roots in temporary Transvaal habitats which had been dry for 18 months. They did not observe this for any Planorbinae (i.e., *Biomphalaria*). Successful aestivation has also been recorded for *Bu. (I.) guernei* (Dautzenberg) in Senegal (Lariviére et al., 1963), *Bu. (Bulinus) forskali* (Ehrenberg) in Kenya (McClelland, 1956), *Bu. (Bu.) senegalensis* (Müller) in the Gambia (Smithers, 1956) and *Bu. (I.) truncatus* in Israel and Iraq by Witenberg & Saliternik (1957) and Zakaria (1955) respectively. Barbosa & Dobbin (1952) and Paraense et al. (1955) reported aestivation by *Bi. glabrata* in Brazil but Pimentel & White (1959) could find no similar evidence for this species in Puerto Rico.

Watson (1958) found that *Bulinus (Isidora) truncatus* in Iraq tolerated dessication for up to 9-10 months in habitats which dried gradually, permitting the snails to form protective epiphragms, whereas rapid drying was usually lethal. Olivier (1956a) found that survival of *Biomphalaria glabrata* and *Bi. straminea* in the field was best in soil with a low moisture content and that prolonged dessication resulted in increased mortality. Barbosa & Dobbin (1952) observed successful aestivation by 32% of a *Bi. glabrata* population in soil with a moisture content varying between 31.5 and 40.0%. Barbosa & Olivier (1958) reported that survival of *Bi. glabrata* was dependant on relative humidity. Decreasing relative humidity was accompanied by an increasing loss of body weight, culminating in death at very low relative humidity levels (0.5%). Snails could survive until they had lost 47-50% of their original weight, but generally they died when this approached 60%.

The influence of relative humidity on drought survival by snails was further emphasized by Sturrock (1970). By simulating expected levels of 4 selected factors (relative humidity, temperature, exposure time and snail size), he showed their effects on St. Lucian *Biomphalaria glabrata* to be interrelated. Using a multiple regression to interpret his data, he suggested that of the individual effects, that of the saturation vapour deficit (thereby excluding the effect of temperature on relative humidity) was the most important and temperature the least so. In the only study on the important question of whether snail eggs can resist dessication, Chernin & Adler (1967) found that *Bi. glabrata* eggs died after even short periods of dessication and under conditions of 90-100% relative humidity. Successful aestivation in dried as opposed to moist mud may depend upon its oxygen content. Coles (1969) found that aestivating *Bulinus (Physopsis) nasutus* required aerobic (i.e., dried) conditions and suggested that the heavy mortalities reported in experiments with moist mud were due to an accumulation of toxic end-products. When dried habitats were refilled, aestivating snails responded by emerging.

Shiff (1960) and Cridland (1967) investigated the survival of Rhodesian *Biomphalaria pfeifferi, Bulinus (Physopsis) africanus, Bu. (P.) globosus* and *Lymnaea (Radix) natalensis* under conditions of controlled temperature and relative humidity. The 3 former species survived fairly hot outdoor conditions for 30-50 days when protected from direct sunlight and particularly in conditions of high relative humidity. *Lymnaea (R.) natalensis*, however, was more susceptible to dessication, even at low temperatures and low relative humidity. This species, nevertheless, laid eggs on damp mud and these remained viable for 20 days. The hatchlings survived in microhabitats until the onset of the rains.

In another comparative study, Lariviére et al. (1962) showed that *Bulinus (Isidora) guernei* could survive for up to 5 weeks under experimental conditions of gradual dessication, whereas with *Biomphalaria pfeifferi* only 50% survived for a month. Chu, Arfaa & Massoud (1967) and Chu, Bijan & Massoud (1967) showed similarly that Iranian *Bu. truncatus* was better able to aestivate than *Bi. alexandrina* or *Lymnaea (Radix) gedrosiana.* Field observations on bulinids by Cridland (1957b), McCullough (1962), Chu, Arfaa & Massoud (1967) and Hira (1968) indicate that medium-sized snails (young adults) survive aestivation best.

Evidence for active entry by the snails into drying substrata is scant. Chu, Massoud & Arfaa (1967), Chu, Massoud & Bijan (1967), Hira (1968) and Lariviére et al. (1962) have reported apparently purposeful penetration into mud under conditions of gradual dessication by several Bulininae, both experimentally and in the field. Hira recorded penetration to a depth of 8 mm. Olivier (1956a) and Lariviére et al. (1962) did not, however, find this ability with either *Biomphalaria glabrata* or *Bi. pfeifferi.*

Bulininae, *Bulinus (Isidora)* and *Bulinus (Physopsis)*, thus appear better able to withstand periods of prolonged dessication (up to a year) and to bury themselves beneath the substratum than members of the Planorbinae (i.e., *Biomphalaria*) or *Lymnaea.*

Olivier (1956b) and Olivier & Barbosa (1956) concluded that the ability of *Biomphalaria glabrata* and *Bi. straminea* to withstand dessication was a characteristic of their habitats rather than of the snails themselves. Those from permanent habitats such as lakes where they could have had little opportunity to develop resistance to dessication did not survive as well as those from temporary pools where drying is a seasonal phenomenon possibly enabling resistant strains to develop. This important finding was confirmed by Colombo (1958), Barbosa & Barbosa (1959) and Kloetzel (1959). Barbosa & Barbosa in fact suggested that the ability of *Bi. glabrata* to aestivate was genetically controlled.

Richards (1967) considered that genetic factors did influence the morphological (i.e., apertural lamellae; Richards, 1964) and physiological changes (i.e., a change in the colour of the digestive gland) in Brazilian *Biomphalaria glabrata* that are associated with successful diapause and prolonged aestivation. This author differentiated between these 2 terms, the former referring to the snails actually leaving the water and entering a state of diapause and the latter to the prolonged survival in a dormant state. There are, according to Richards (1968), no true breeding lamellar strains, which points to the possession of this characteristic (associated with the ability to aestivate successfully) by some snails as a genetic mechanism ensuring that part of a population in a temporary habitat will survive the dry seasons.

Although lamellae have been reported in *Biomphalaria glabrata* from Brazil (Paraense, 1957) and in *Bi. pfeifferi* from Ghana (McCullough, 1958), no lamellar *Bi. glabrata* have been found on St. Lucia (Sturrock, 1970), a strain which Sturrock considered adapted poorly to withstanding dessication. Likewise, no lamella-bearing *Bi. pfeifferi* have been reported among southern African populations so far, although this character may not have been looked for.

While many species of the genera *Bulinus* and *Biomphalaria* are known to be able to aestivate, some for considerable periods, neither Rhodesian nor South African *Bi. pfeifferi* have been recorded doing so under natural conditions, although this has been demonstrated in the laboratory (Shiff, 1960; Cridland, 1967).

LIGHT

Practically all observations on the influence of light on host snails are qualitative. *Biomphalaria glabrata* occurs in both shaded habitats and those exposed to direct sunlight, whereas African host snails appear to avoid the latter. Most host snail species have, nevertheless,

been recorded as able to survive for several consecutive generations in almost total darkness (Deschiens & Bijan, 1956; Deschiens, 1957a; WHO, 1957; Watson & Ali-Ali, 1961). Boycott (1936), Mozley (1939), Zakaria (1955), Malek (1958) and Watson (1958) suggested that the effect of sunlight is an indirect one, related to photosynthesis and the availability of food.

Cooke (1895), quoting experiments by Willem in 1892, and Boettger (1944) suggested that planorbids and lymnaeids may be negatively and positively phototaxic respectively. Dainton (1954a,b), Karlin (1961), DeWitt (1967) and Hunter (1968) have reported nocturnal locomotor, feeding and egg-laying patterns for a variety of aquatic and terrestrial Pulmonata. However, they considered these activities to be due to changing temperatures rather than light intensities. Others, Newell (1968) and Lewis (1969a,b), believe that daily photoperiods are more important in controlling locomotor activity than temperature changes, while Imhof (1973) suggests that both play roles in determining the intrinsic rhythms of growth and reproduction.

Joy (1971) found that *Biomphalaria glabrata* laid its eggs at night, but Sodeman (1972) failed to detect any obvious influence on the species' activity due to changes from light to dark conditions and vice versa. Several authors (Gordon et al., 1934; Deschiens & Bijan, 1956; Stiglingh & van Eeden, 1970; Pitchford, pers. comm., 1975), however, have remarked on the congregation of planorbid host snails on the surfaces of bodies of water during the hours between sunset and sunrise. This phenomenon was also noticed by me among snails in outdoor aquaria at Lake Sibaya Research Station (northeastern Natal) in 1973. Observations on *Bulinus (Physopsis) globosus* there revealed a regular nocturnal activity pattern and that most eggs were laid at night. The snails emerged from behind shelters between 1400 and 1700 hrs. after temperatures had begun to fall and light intensities started to decrease. They returned at about 0600 hrs. when temperatures and light intensity began to increase. No difference was noted in this behaviour pattern between days with plentiful cloud cover (only 3.5 hrs. direct sunshine) and those without (8.6 hrs. direct sunshine and the maximum for the season). This pattern, which corresponds well with that reported by Lewis (1969a) for the terrestrial slug *Arion ater* (Linnaeus), appears to be independent of the direct (global) fraction of sunshine, but is possibly dependent upon either the diffuse fraction or temperature or both. Further observations under controlled conditions should help elucidate this.

The planorbid eye conforms to the general pulmonate pattern in being a closed vesicle with a spheroidal lens (Cooke, 1895; Boettger, 1944; Pan, 1958; Charles, 1966). There is very little vitreous humour, so that the retinal cells lie extremely close to the lens. This, coupled with the apparent absence of any accomodatory apparatus probably causes images of distant objects to form behind the retina. Form vision will therefore be unlikely, especially under water. Nevertheless these eyes and the dermal photoreceptors are efficient in detecting even small changes in light intensity and may therefore be expected to play an important role in the snails' behaviour pattern. Some degree of colour discrimination is probable and there is evidence (Boettger, 1944) that lymnaeids, and possibly planorbids as well, avoid red light. Joy (1971) has in fact demonstrated greater egg production by *Biomphalaria glabrata* under experimental lighting from which infrared wave lengths were absent than under conditions which included red light. Since daylight contains abundant red light, whereas moonlight lacks these wave lengths to a large extent, this may explain in part the apparently nocturnal activity of many Pulmonata, including the bilharziasis host snails. The likelihood of bilharziasis host snails exhibiting such a behaviour pattern does not seem to have been taken into account, except by Joy (1971), and could be an important aspect of their ecology.

STREAM GEOLOGY

Mozley (1939) and the WHO Study Group (1957) have pointed out that the physiography of a region influences the diversity, abundance and size of freshwater habitats and therefore the occurrence of snails as well. The concept of geomorphology affecting the distribution of fluviatile organisms in this way is not new, but except for a series of papers on the physiographic aspects of *Biomphalaria glabrata* ecology in Puerto Rico (Harry & Cumbie, 1956a,b; Harry & Aldrich, 1958; Pimentel & White, 1957, 1959), no serious attempt has been made to correlate host snail distribution with the distribution and properties of the bedrock making up their habitats.

Appleton (1975) has postulated the existence of a relationship between the occurrence of *Biomphalaria pfeifferi* and *Bulinus (Physopsis) globosus* and low gradient stretches of watercourses over rocks with hardnesses of 5 or greater in Mohs' Scale of Hardness in the southeastern Transvaal. These rocks, mostly granites, are resistant to erosion and weather unevenly, resulting in the formation of lentic habitats detached from the channel. Substrata of these resistant rocks are more stable than those of non-resistant rocks or sand and are less porous. These qualities both contribute to an important factor determining host snail distribution — habitat permanence.

The nature of the substratum itself as a factor has not been emphasized as being of much importance. Firm mud, usually rich in decaying organic matter, is the type of substratum generally associated with host snail habitats (van Someren, 1946; Malek, 1958; Watson, 1958; Gohar & El Gindy, 1960a), although whether there is any substratum-controlled distribution of snails within a particular body of water is not known. Meillon et al. (1958) suggested that the degree of compactness of the substratum might be more important to the snails than its organic content. Van Eeden & Combrinck (1969) could, however, find no active selection of substratum types by *Bulinus (Isidora) tropicus* and *Lymnaea (Radix) natalensis* under experimental conditions. Clampitt (1973) found in a North American lake that while some Pulmonata did show statistically significant preferences for particular substrate types, others did not. He stressed that most species exhibit considerable plasticity in their occurrence on different substrata and that what applies for one species in one situation may not apply for that species in another. The availability of food and firm surfaces for oviposition may be modifying factors in substrate selection.

SUMMARY

A feature of this extensive literature is the abundance of 'anecdotal' descriptions of the effects of abiotic factors on host snails and their life cycles. Though these provide essential base line data, the dearth of truly quantitative evidence from both field and laboratory represents a shortcoming. Quantitative data is vital in order to assess objectively which factors are important, since, as Jordan & Webbe (1969) have stressed, the ecological requirements of the various host snail species are qualitatively similar but quantitatively different. Available evidence indicates that 2 factors, temperature and current velocity, are largely responsible for the snails' present distribution patterns in southern Africa.

Fundamental differences have been shown to exist between the tolerances of members of the Bulininae and Planorbinae. *Bulinus (Physopsis) globosus*, for instance, is tolerant of a wider range of calcium and bicarbonate ion concentrations and temperature and of longer dessication than *Biomphalaria pfeifferi*, although *Bulinus (Isidora)* is able to aestivate for still longer periods than *Bulinus (Physopsis)*. There is experimental evidence that *Bu. (P.) africanus* is better adapted to cooler conditions than *Bu. (P.) globosus*. These findings are reflected respectively in the restricted distribution of *Bi. pfeifferi* compared with that of *Buli-*

nus (Physopsis) and the allopatric distributions of *Bu. (P.) africanus* and *Bu. (P.) globosus* in southeastern Africa.

Recent experiments indicate that *Bulinus (Physopsis) africanus* is able to acclimate to natural waters of widely different chemical quality. Such an ability is probably possessed by the other planorbid host snails to a greater or lesser degree and explains the observations from many countries that water quality within the range of ionic composition normally found in field habitats seldom approaches levels lethal to snails and cannot therefore be regarded as an important limiting factor to them. However, water quality does influence the snails' local abundance.

Host snails have also been collected in water ranging widely in temperature. Quantitative studies have shown not only that host snails can survive, albeit with varying measures of success, over a wide range of temperatures, but that both the upper and lower limits for population survival lie at levels commonly recorded in natural bodies of water. This has been found to be important as a limiting factor to *Biomphalaria pfeifferi*. Whether it applies to *Bulinus (Physopsis)* is not yet known. Species which have a high and well-defined optimal temperature for population expansion appear to be better able to survive in temporary habitats than those with lower and ill-defined optimal temperatures (i.e., southern African *Bi. pfeifferi*) which favour permanent habitats and are thus uncommon in areas subject to a markedly seasonal rainfall (i.e., the highveld plateau of southern Africa).

Another important factor is current velocity. *Bulinus* and *Biomphalaria* occur only in lentic habitats and in waters flowing at velocities of up to 0.3 m/sec. This narrow tolerance range of 0-0.3 m/sec. restricts the longitudinal distribution of these snails in river systems and renders large parts of these watercourses uninhabitable despite water quality and temperature being suitable. In river systems current velocity is an important limiting factor while temperature has a subordinate influence, though in headwater reaches the latter may be the more significant.

Water velocity is determined largely by geomorphic factors, in particular the resistance offered to erosion by different types of bedrock, and suitable lentic habitats develop in natural watercourses only on rocks with hardness values ≥ 5 in Mohs' Scale of Hardness. The significance of this factor, which determines the permanence of habitats in terms both of their confines and permeability, has been demonstrated by Appleton & Stiles (1976). They have shown that the cartographical distribution of host snails in South Africa corresponds closely with that of geological formations comprised largely of rock types resistant to erosion.

Temperature thus emerges as the abiotic factor which, according to available evidence, is of greatest importance in determining the distribution of host snails in lentic environments (i.e., ponds and lakes). Current velocity is the most important factor in lotic environments (i.e., river systems).

Reference to other branches of ecology can improve the usefulness of measurements of abiotic factors. The relevance of the components of level and duration in studies on the effects of abiotic factors has often been noted. Macan (1958) discussed the use of degree hours in limnology and demonstrated that by defining a temperature base line the value of this parameter is greatly enhanced. Using 'Effective Temperature' Stuckenberg (1969) has shown the importance of environmental conditions during breeding seasons in determining the distribution of poikilothermic, terrestrial animals. Ainslie (1973) has indicated the advantages of expressing abiotic marine factors as exceedance frequencies. The adoption of methods such as these should hasten the practical application of knowledge on factors which limit the distribution of the bilharziasis intermediate snail hosts and enable the likelihood of their spreading to new areas to be assessed. This last facet is important today when impressive irrigation schemes are being built in developing countries, sometimes in areas non-endemic for bilharziasis without much regard to their impact on, amongst other things, the epidemiology of water-borne diseases.

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NONMARINE MOLLUSCS IN QUATERNARY PALEOECOLOGY[1]

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ABSTRACT

Precision in reconstruction of Quaternary environments using nonmarine molluscs is related to the degree of certainty with which fossil material can be referred to living species. Knowledge of a demonstrated, implied or inferred relationship between living species and the environment, in which the effects of the interaction are expressed as limitation of geographic range, and/or phenotypic variation in shell morphology or composition, form a basis for environmental interpretations.

Many such interactions have been described in the literature. These include: (1) distribution patterns related to temperature and available moisture; (2) variations in shell size that have been attributed to current, wave action, temperature and altitude; (3) increase in shell thickness and reduction in aperture size in response to increased aridity; (4) the tendency of some species of hydrobiids to develop spines in response to increased salinity; and (5) variation in isotopic and trace element composition of shell material that have been related to temperature and vegetation changes in the local habitat.

Limitations in the use of nonmarine molluscs are imposed by the uncertainties involved in the identification of certain species from shell material, inadequacy of distributional and ecological data for many living species, and the very real possibility that the evolution of some physiological changes may have occurred in some species even though there may be no recognizable changes in shell morphology.

INTRODUCTION

Precision in reconstruction of Quaternary environments using nonmarine molluscs is related to the degree of certainty with which fossil material can be referred to living species. Knowledge of a demonstrated, implied or inferred relationship between living species and the environment, in which the effects of the interaction are expressed as limitations of geographic range, phenotypic variation in shell morphology or shell composition, form the basis for environmental interpretations.

This paper reviews some of the ways in which nonmarine molluscs could be used to obtain information about Quaternary environmental conditions, the rationale behind some of these methods, and their limitations.

GEOGRAPHIC DISTRIBUTION

The majority of the studies involving Quaternary nonmarine molluscs have been concerned with deriving information about the local climate from the distribution patterns of living species. The methods generally used in these analyses involve comparison with the modern molluscan fauna occurring in the same region as the fossils, or by comparison with an extant fauna from some other region which contains faunal elements that are similar to those found in the fossil assemblage (Taylor, 1960, 1965; Miller, 1966). Some analysts have

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grouped molluscs on the basis of their distribution pattern and plotted changes in the abundance of these climatically significant species groups to interpret climatic changes (Sparks, 1961; Miller, 1975, 1976a). Implied in these methods of analysis is the assumption that some aspects of climate are responsible for the frequently observed differences between the modern fauna and Quaternary fossil assemblages found within the same area.

Temperature extremes and available moisture appear to be the 2 major climatic factors controlling the distribution of nonmarine molluscs (van der Schalie & Berry, 1973; Randolph, 1973; Elwell & Ulmer, 1971; Taylor, 1960; Clarke, 1973; Miller, 1975). Interpretations predicated on these simple assumptions have generally not been in conflict with conclusions reached independently from studies based on other fossils found associated with the molluscs.

For certain groups of nonmarine molluscs, for example the unionids, changes in distribution are almost certainly related to other factors besides temperature and suitable aquatic habitats. The successful establishment of a unionid species in a new drainage requires not just accessibility and compatibility of the physical and chemical conditions in the new area, but also demands the successful establishment of the species of fish which serves as obligatory host to the ecto-parasitic glochidium stage that unionids pass through to complete their life cycle. The dispersal of the host fish and of the intimately associated unionid species is believed to require confluence of drainage systems (van der Schalie, 1945, 1963). Unionids, therefore, are potentially useful in reconstructing the former drainage pattern of a stream.

Miller (1970; 1976b) has used the modern and fossil occurrence of certain unionid species to infer former connections between the upper Smoky Hill, the Neosho-Verdigris and Marais des Cygnes Rivers. Prior to the Kansan Stage, the Upper Smoky Hill River is believed to have drained south through McPherson Buried Valley, as a tributary of the ancestral Arkansas River (Bayne & Fent, 1963). Headward erosion by the ancestral Kansas River captured the Upper Smoky Hill during or soon after the Kansan Stage (Murray & Leonard, 1962). The fossil record of unionids from the Upper Smoky Hill, however, suggests that prior to its capture by the Kansas River, but after the McPherson Channel was abandoned, it

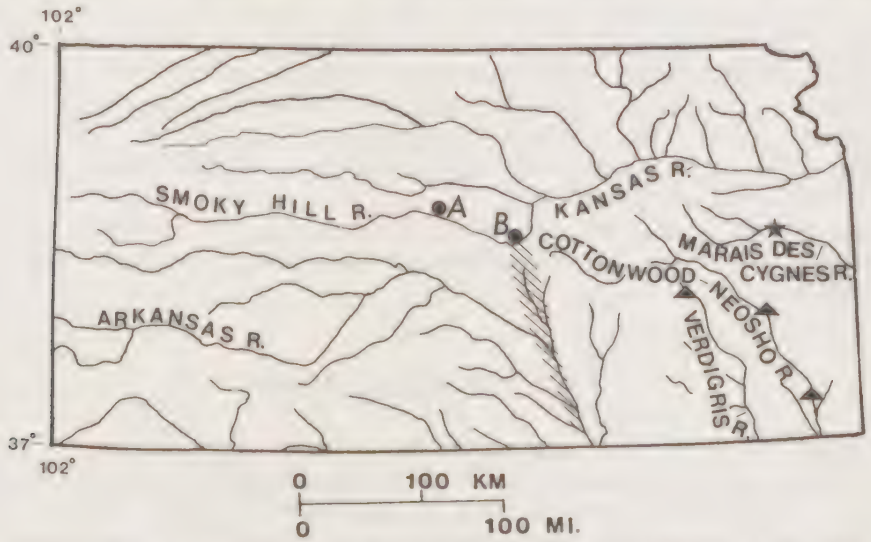

FIG. 1. Drainage map of Kansas showing the location of the Kanopolis local fauna (A), and the Sandahl local fauna (B) along the Smoky Hill River. The triangles represent modern records of *Pleurobema cordatum catillus* in the Cottonwood-Neosho and Verdigris drainages. The star represents the 1 modern record of *Arcidens confragosus* in Kansas. The diagonal lined pattern shows the approximate location of the McPherson Buried Valley.

may have been in confluence with the Neosho-Verdigris and Marais des Cygnes drainages (Fig. 1). *Pleurobema cordatum catillus* and *Arcidens confragosus* do not now occur in the Kansas River drainage, but are restricted in Kansas to the Neosho-Verdigris and Marais des Cygnes drainages, respectively (Murray & Leonard, 1962). *P. c. catillus* occurs as a fossil in the Sandahl local fauna (Miller, 1970) and *A. confragosus* has been identified in the Kanopolis local fauna (Miller, 1976b). Both fossil occurrences are from terrace sediments deposited by the ancestral precursors of the Smoky Hill River and imply former connections between the Upper Smoky Hill and the Neosho-Verdigris and Marais des Cygnes drainages.

FAUNAL ASSOCIATIONS

A more reliable perception of paleoecologic conditions can usually be obtained when an entire assemblage, rather than a single species, provides the basis for the reconstruction.

Although most Quaternary faunas are mixtures of several different communities, there are numerous recurring associations of species which permit recognition of specific habitats. In most reconstructions the habitat groupings are based on the known or assumed habitat preferences of modern species (Hibbard & Taylor, 1960; Miller, 1966). Some studies have utilized rigorous quantitative statistical techniques to provide useful environmental data. Pauken (1969; 1971) generated habitat-moisture indices from species abundance, diversity and habitat preference in his study of loess fossils in Missouri. His analysis of these data identified 2 distinct groupings at different stratigraphic levels and at different geographical localities: (1) a prairie, prairie-forest border community fauna; and (2) an upland deciduous forest fauna. Variations in the vertical and lateral distribution of these groups led him to conclude that from the Late Pleistocene to the present an upland forest existed in Missouri which underwent periodic east-west shifts in response to climatic change. Gould (1969a) used R-mode and Q-mode multivariate analysis to distinguish 4 reoccurring terrestrial molluscan assemblages from the Pleistocene of Bermuda. He was able to relate these communities to inferred climatic changes which controlled the amount of carbonate in the substrate.

SHELL SIZE AND MORPHOLOGY VARIATION

Although an extensive literature exists dealing with the effect of environmental factors on shell morphology, relatively few studies have made use of these relationships in the interpretation of Quaternary assemblages (Gould, 1969b; 1971a).

Shell Size. In many freshwater molluscan species shell size appears to be related to the nature of the aquatic environment. Ortmann (1920), van der Schalie & van der Schalie (1950), Cvancara (1963) and Matteson (1953) have noted that some species of unionids generally increase in size and obesity in the downstream direction. In lentic environments subjected to strong waves or in lotic habitats subject to strong current action, shells frequently become reduced in size. Reduction in shell size in response to one of these external environmental factors has been noted in the hydrobiids (Berry, 1943), in the unionids (Brown et al., 1938), in the pleurocerids (Weibe, 1926), and in the lymnaeids (Clarke, 1973). Berry (1943) has suggested that the stunting may be due to agitation of the water which causes the animal to withdraw its body and mantle into its shell and cease accreting shell, to shorter growing seasons (lake forms tend to be smaller than river forms perhaps because ice remains longer on the lakes), or to water temperatures which are lower than those to which the organism has adjusted. Matteson (1960) and Parmalee (1968) have used this assumed temperature-size relationship to interpret collections of dwarfed unionid shells from 7,000- to 8,000-year-old Archaic sites in Illinois. The species, which with few exceptions typically occupy cold water,

were noticeably smaller than representatives of the same species found at younger sites or that are still living. The smaller size shells were attributed to a shorter growing season due to lower average temperature during this time interval.

Terrestrial snails also show size and shape variations that have been attributed to some environmental factors. Gould (1971b), for example, noted that 4,000-year-old subfossil shells of *Cerion* from the Dutch Leeward Islands are significantly larger than members of the genus now living in the same area. Gould considered the large size of the subfossil material to be either a response to a more hospitable climate during that time, or that the population was a relict that had adapted to the pluvial conditions of a previous glaciation. In either interpretation large size was associated with optimal growing conditions.

Archer (1948) observed that many species of *Stenotrema* undergo a relative increase in width and decrease in shell height from higher elevations to lower altitudes. Van der Schalie (1948) described stunting in several terrestrial species of Puerto Rican snails in which the severity of dwarfing increased with altitude.

Shell Morphology. There are numerous accounts relating environmental conditions to variation in the shell morphology of many molluscs. Te (1975), in his recent study of the Michigan Physidae, recognized conchologically distinct "ecological subspecies." Environmental control of shell shape is implied in his use of this taxonomic category. Basch (1963a; 1963b) has shown that stunting and distortions in the shell of the aquatic pulmonate snail *Ferrissia fragilis* can be caused by drying up the environment. *F. fragilis* var. *shimekii* is a septate form of this species which occurs in some individuals of populations that are subjected to periodic drought. The function of the septum apparently is to reduce the size of the apertural opening and thus diminish the amount of water lost from the body when the animal withdraws into the shell during episodes of dessication. Septate forms of *F. fragilis* are known from the fossil record (for example, the Kanopolis local fauna (Yarmouth?), Ellsworth County, Kansas) and their presence can be considered *prima facie* evidence for the existence of temporary water habitats which are subject to periodic drying.

Cessation of shell growth occurs in other molluscs in response to drought and/or to drastic temperature changes. Numerous growth interruption lines may form in a single year in this way. In more stable water bodies such as large lakes and rivers, the shells of unionids frequently develop annuli which are believed to represent yearly growth-interruptions (Coker et al., 1921). These might serve as a method for estimating the age and relative rates of growth in fossil populations.

Vagvolgyi (1968) noted in his study of *Triodopsis* that the development of a heavy parietal lamella was usually associated with species occurring in mountainous areas. He could not, however, offer any functional explanation for this adaptation.

Some prosobranch freshwater snails (e.g., *Potamopyrgus jenkinsi* (Smith)) develop spines, keel or carinae in response to increase in salinity (Real, 1973; Warwick, 1969). Leonard & Franzen (1944; 1946) have interpreted the presence of these features on shells of the closely related genus *Calipyrgula* from the lower Pliocene Laverne Formation of Oklahoma as an indication that the lake or lakes in which these organisms lived became periodically brackish.

Unfortunately, the reported relationships between shell-size or shell-form and environmental factors are frequently little more than *ad hoc* attempts by authors to explain shell variation observed in their samples. Relatively few studies have been designed to establish quantitative relationships between shell variation and the environment. Potentially useful paleoecologic data, however, have been obtained when the primary purpose of the investigation was the study of the effects of environmental vicissitudes on the shell. Machin (1967) has described shell modifications in 3 terrestrial helicids (*Helix aspersa, Otala lactea* and *Sphinceterochila boissieri*) that have geographic ranges that include arid regions. In desert environments the shells of these species tend to increase in thickness, decrease in surface area, and develop smaller apertures to reduce water loss.

Couri (1976) studied 356 specimens from 14 populations representing most of the modern range of *Gastrocopta procera* to determine if variation in shell morphology could be related to climatic factors. Statistically significant correlations were found which associate shell height, number of whorls (Fig. 2), angle of the lower palatal lamella (Fig. 3), and width

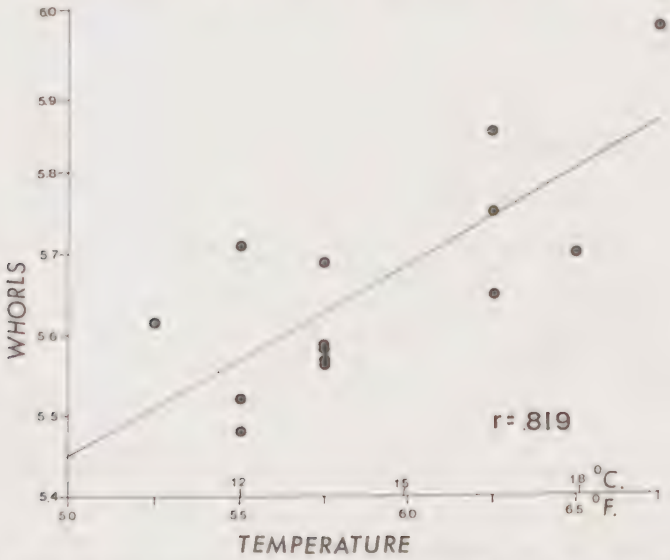

FIG. 2. Scatter diagram of 14 modern populations of *Gastrocopta procera* showing correlation between (r = .819 @ .005 significance level) the number of whorls to the average annual temperature (after Couri, 1976).

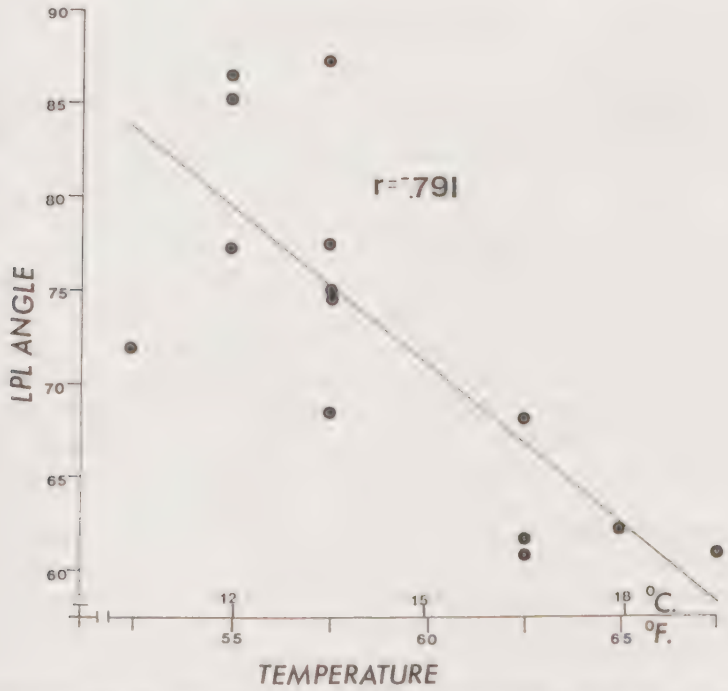

FIG. 3. Scatter diagram of 14 modern populations of *Gastrocopta procera* showing correlation between (r = -.791 @ .005 significance level) the lower palatal lamella angle and the average annual temperature (after Couri, 1976).

TABLE 1. Correlations between shell morphology and factors of climate[1].

Climatic variable	Height	No. whorls	LPL angle
Mean growing season (annual no. frost-free days)	NC	.694 (.005)	-.659 (.025)
Average date, last killing frost	NC	-.663 (.005)	.669 (.005)
Average date, first killing frost	.571 (.025)	.539 (.025)	-.461 (.050)
Average depth of frost penetration	-.975 (.005)	-.530 (.025)	NC
Average annual temperature	.737 (.005)	.819 (.005)	-.791 (.005)
Average July temperature	NC	.781 (.005)	-.889 (.005)
Average summer precipitation (June - August)	-.774 (.005)	-.535 (.025)	NC

[1] Each correlation coefficient is accompanied by the significance level in parentheses. NC = no correlation obtained (after Couri, 1976); LPL = lower palatal lamella.

with temperature and to a lesser degree with precipitation (Table 1). These aspects of morphology are currently being studied in fossil *G. procera* to determine if they can be used to extract climatic data.

SHELL COMPOSITION

The isotopic composition of the carbonate in the shell of freshwater molluscs may provide information on the environment. Weber & La Rocque (1963) found that gastropods living in environments occupied by dense pond weed vegetation, which fractionate C^{12}/C^{13} in favor of the lighter isotope, tend to have a predominance of the lighter isotope in their shell. Snails living in open waters that are essentially free of vegetation have C^{12}/C^{13} ratios which are much like the typical values for freshwater carbonate.

Stuvier (1968), in a study of the O^{18}/O^{16} ratio in freshwater carbonate and mollusc shell from a core taken from Pretty Lake, Indiana, found that variations in the average isotope ratio of the lake water was less than 1 per mil in this area during the last 9,000 years and that therefore the O^{18} content of the lake water and thus of atmospheric precipitation only fluctuated within narrow limits. From this he concluded that atmospheric circulation patterns over the Great Lakes Region had remained essentially stable during the last 9,000 years.

Fritz et al. (1975) studied oxygen and carbon isotopes in molluscs and sediments from a long core in Lake Erie. Their isotopic analysis identified 2 major climatic improvement events, one occurring between 13,000 to 12,000 years before the present (B.P.) and a 2nd between 10,000 and 8,000 years B.P. Although oxygen isotope studies in freshwater systems apparently cannot be directly calibrated to temperature, they can be used to identify climatic trends involving temperature changes.

The work of Ho (1966) suggests that the nitrogen content of water insoluble residues from shell protein of nonmarine molluscs might be used for estimating temperature and moisture conditions in an area since the time the shell became buried. The technique is based on the hydrolysis rate of shell protein which is dependent on moisture and temperature. If the

age of the shell material can be established, the relative effect of moisture and temperature can be estimated. Although the method does not produce quantitative moisture or temperature values, it can serve as a basis for evaluating relative moisture and temperature conditions between faunas from the same climatic region. A similar technique using amino acid diagenesis has been used with some degree of success by Mitterer (1974; 1976) in the analysis of marine Cenozoic molluscs from the Atlantic Coastal Plain.

The longevity of some species of unionids together with their ability to incorporate small quantities of trace elements from the environment into their shell has spurred investigation in their use as minitors of chemical conditions in aquatic environments (Saville & Sterrett, 1974). Such studies have increased the potential use of these organisms in reconstructing some of the chemical parameters in Quaternary aquatic environments. Nelsen (1967), for example, has studied the microchemical constituents in modern and subfossil unionid shells from the Tennessee and Clinch Rivers. He found that concentrations of Sr, Ba, and Mn in the subfossil shells of *Elliptio crassidens* were 100% greater than in contemporary shells. He attributed the changes to cutting of the forest cover which changed the rate of chemical weathering and ultimately altered the concentrations of weathering products carried by groundwater and surface runoff into streams.

Kovach (1977) studied the concentration of Mn in the shells of 13 species of recent unionids. He found that shells from impounded environments commonly contained twice the Mn concentrations of shell from moving water riverine situations. His work suggests the possible use of this relationship for identifying lentic and lotic environments in the fossil record.

Variation in the ratio of calcite to aragonite in the shell of certain species of mollusc suggest the possible correlation of environmental temperature and crystal type. Wilbur (1964) measured changes in the ratio of calcite, aragonite and vaterite in regenerated shell of *Viviparus intertextus* and found that the proportion of aragonite increased with temperature. Although aragonite frequently recrystallizes to the more stable calcite form in fossil material, the technique is potentially usable because the original aragonite can be preserved under certain conditions. The X-ray diffraction pattern of fossil shell from the Late Pliocene Rexroad local fauna (Taylor, 1960), for example, showed almost pure aragonite, and therefore one might assume that the original shell was also composed mostly of aragonite.

LIMITATIONS

The starting point for paleoecologic interpretations of Quaternary nonmarine assemblages is the tacit assumption that fossils assigned to still living taxa have undergone little or no evolutionary change (Taylor, 1965). There is, however, some data which questions the validity of this assumption. Evolutionary changes in *Gastrocopta procera* are suggested by Couri (1976). Couri's study of Holocene *G. procera* indicate a change in the relationship between certain shell morphologic features. Modern shells, for example, show a negative correlation ($r = -.829$) between the number of whorls and lower palatal lamella angle. This correlation does not occur in the fossils from the southwestern Kansas-northwestern Oklahoma region (Fig. 4).

There are too many cases of taxonomic instability among some groups of nonmarine molluscs which make accurate placement of fossil material uncertain and the application of accumulated ecologic data for some species of questionable value. Walter (1969), for example, concluded that *Stagnicola elodes* and *S. emarginata* were only extreme variants of the same species and that all of the nearly 60 North American species of *Stagnicola s.s.* ought to be taxonomically united under the name *Lymnaea catascopium* Say. Burch & Ayers (1973), however, found that *S. elodes* and *S. emarginata* could not be cross-fertilized and concluded that they were probably good species and not simply ecophenotypes.

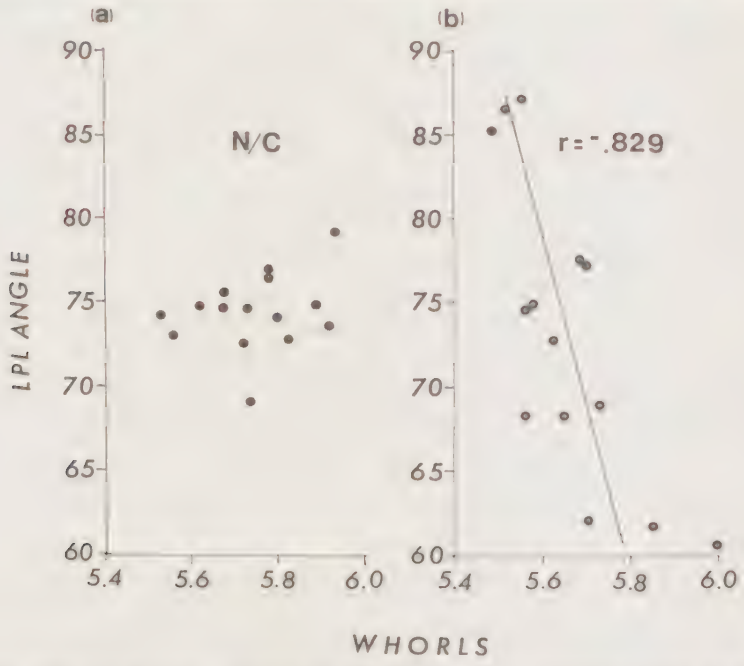

FIG. 4. Scatter diagrams showing relationship between (a) lower palatal lamella angle and the number of whorls in 15 fossil (no correlation) and (b) 14 modern (r = -.829 @ .005 significance level) populations of *Gastrocopta procera* (after Couri, 1976).

Most Quaternary assemblages are thanatocoenose and contain a mixture of many habitats. The contemporaneousness of such assemblages is an assumption which is subject to modification or rejection as the evidence warrants.

Taylor (1965) considered the worn and etched condition of most of the shells from the Rezabek local fauna, Lincoln County, Kansas (in contrast to the normal fresh condition of shells usually found in Pleistocene faunas of the area) as evidence of probable reworking from older Pleistocene deposits and recommended that the molluscs be ignored in the interpretation of this assemblage. In another example involving the probable mixing of faunas, I recommended that the molluscs of the Java local fauna (Martin, 1973) not be used in interpretation of the fauna because of (1) the crushed and rehealed condition of some of the shells, (2) the dark-grey to black color of the rehealed shells in contrast to the color of the uncrushed materials, (3) the occurrence of several shells belonging to Cretaceous or Paleocene marine gastropods, and (4) the occurrence within a coarse sand matrix of fine sand and silt clasts which appeared to have been transported as discrete fragments.

Circumstances associated with the collection of fossil molluscs often place serious constraints on their use in the interpretation of nonmarine sequences. With few exceptions (see, for example, Bickel, 1970; Camp, 1974), molluscs have not been actively sought and are often collected because of their presence in the remaining residue after vertebrate and/or archaeological materials have been removed. Assemblages from many archaeological sites are incomplete because the smaller faunal elements pass through the screens. Even the finer (16-mesh) screen utilized by vertebrate paleontologists collecting microvertebrates will lose many of the smaller molluscs such as *Carychium exiguum* and *Gastrocopta pellucida hordeacella.*

CONCLUSIONS

A number of assumed cause-and-effect relationships between environmental factors and shell morphology have appeared in the literature which are potentially useful in paleoecologic interpretations. Some of these relationships, such as the development of an apertural septum in *Ferrissia* in response to dessication, appear to be adequately documented, whereas other interactions, like the reported reduction in shell size due to low temperature, wave or current action, appear to be in need of further verification before they can be used as reliable guides for the interpretation of fossil assemblages.

Paleoecologic reconstructions of fossil assemblages are obviously strongly dependent upon knowledge of modern species. The strength of this dependency was emphasized by Taylor (1965) in his review of the state of Pleistocene malacology in North America. The gist of his concluding remarks was that if paleontological study of Pleistocene mollusks suffered then from lack of basic biological research, it would do so to a much greater degree in the immediate future . . . "Conventional conchological-stratigraphic research had proved to have some use, but in the long run strictly zoological study would advance Pleistocene paleontology more."

Increased interest in man's impact on the environment has spawned a number of studies which are contributing basic biologic data on nonmarine molluscs. Van der Schalie & Berry's (1973) examination of the effects of temperature on the growth and reproduction in aquatic gastropods, Yokley's (1972) investigation of the impact of impoundment and pollution on unionids in part of the Tennessee River, and Mathis & Cummings' (1971) study of the distribution of metals in clams, sediments, worms and fish from the Middle Illinois River are examples of this type of research.

Some of the problems posed by an unstable taxonomy are being resolved. The work of Burch & Lindsay (1972a; 1972b) on the lymnaeids, Te (1974; 1975) on the physids and Patterson (1971; 1973) on the succineids indicate that there are an increasing number of investigations directed at establishing some taxonomic order to groups that have been notoriously unstable.

The prospectus for Quaternary studies of nonmarine molluscs does not appear to be quite as bleak today as it did to Taylor in 1965. Although Pleistocene malacology continues to rely heavily upon information gained from the study of living molluscs, the interpretation of fossil assemblages is certainly not completely dependent upon such knowledge. The relative ease with which large numbers of fossils can frequently be collected encourages the use of multivariate statistical analysis. These techniques can be used to identify relationships between a complex of variables expressed as variation in shell morphology, species abundance, species diversity and species associations, and environmental factors. The study of reoccurring assemblages of land snails in the Pleistocene sequence of Bermuda, which Gould (1969a) was able to relate to climatic oscillations, and Shaak's (1976) investigation of lacustrine sediments in the Pleistocene of Oklahoma, in which he was able to explain changes in species diversity and species abundance within the aquatic molluscan community as a response to normal lake succession, are examples of how considerable amounts of paleoecologic information can be extracted from fossil-sediment associations without relying on detailed knowledge of the ecological requirements of the species involved.

Greater precision in the reconstruction of Quaternary environments should result from acquisition of basic new data on the biology of nonmarine molluscs and from the increased application of statistical analytical techniques that can extract simplified relationships from a confusing array of variables.

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LABORATORY OBSERVATIONS ON THE EGGS AND YOUNG OF *TRIODOPSIS ALBOLABRIS MAJOR* (PULMONATA: POLYGYRIDAE)

Virginia A. Vail

ABSTRACT

Observations on *Triodopsis albolabris major* (Binney) over 2 consecutive reproductive seasons provided information on the number of egg clutches per individual per season, egg size, number of eggs per clutch, duration of incubation, size of newly hatched young and growth rates. Adults generally oviposited at least twice during a reproductive season. Egg size averaged 4.70 x 4.28 mm, with an average of 62.3 eggs per clutch. The young, hatching out after approximately 21 days, had a shell diameter approximately 1/10 that of adult specimens. The young attained adult size and oviposited within 1 year.

INTRODUCTION

Simpson (1901) and Pilsbry (1940) described the reproductive anatomy of several *Triodopsis*, but there have been few prior studies of reproductive performance in this genus of land snails. Ingram (1944) described the process of egg laying in *T. dentifera* (Binney). Ingram (1944), Gugler (1963) and Kingston (1966) presented brief observations on the eggs of *T. dentifera* and *T. tridentata* (Say), *T. albolabris* (Say), and *T. multilineata* (Say) and *T. dentifera*, respectively. Egg size, number of eggs per clutch, number of clutches per individual, duration of development, hatching and the young were, at most, only superficially examined in those studies, and the purpose of this report is to describe those features in *T. albolabris major* (Binney).

MATERIAL AND METHODS

Twenty-one mature specimens of *Triodopsis albolabris major* were collected in late March 1975 on Greenwood Plantation, near Thomasville, Thomas County, Georgia, U.S.A. Their shells averaged 36.7 ± 1.45 mm in diameter and 23.8 ± 1.39 mm in length. Identification of this species was based on Pilsbry's (1940) description and on comparisons to specimens in the Academy of Natural Sciences of Philadelphia. Voucher specimens, including eggs and shells of juveniles, have been deposited in that institution (catalogue number: 342092a,b,c,d).

Specimens were numbered for individual identification with water-proof black drawing ink and kept in pairs in plastic shoe boxes with wet paper toweling until December 1975. At that time, for convenience, specimens were transferred to 2 15-gallon aquaria with a 5 cm layer of soil substrate. The animals thrived on a diet of lettuce greens, carrots, cucumbers and wild mushrooms of the genus *Russula* (when available). Pieces of limestone, as a source of calcium, also were made available to the snails.

All specimens were observed frequently for signs of copulation and oviposition. Egg clutches were removed from the parental container and placed on moist paper toweling in petri dishes to facilitate observations and measurements of the eggs during development and hatching. The hatchlings from each clutch were kept together in plastic shoe or sweater boxes and given the same foods as the parental stock. Shell measurements of the hatchlings were taken at 4-week intervals (28 days), commencing with hatching.

Measurements of eggs and juveniles 10 mm or less in diameter were made with a calibrated ocular micrometer; measurements on snails greater than 10 mm diameter were made with vernier calipers. Diameter measurements on adult shells did not include the reflected lip of the aperture in order to better compare adult shell size with that of the juveniles which lacked the reflected lip. Inclusion of the reflected lip would have increased the diameter measurements by 1-2 mm.

Average measurements cited in the text and Table 1 are generally accompanied by the standard deviation.

OBSERVATIONS

In the field, the reproductive season probably occurs during the warmer months of the year (May through September or early October). It is also possible that above-normal winter temperatures can extend the reproductive season. Although eggs and very young snails were difficult to find in their habitat, some field observations are available to support the above hypothesized reproductive season. Small juveniles (approximately 1/3 adult diameter) were found in late March 1975, during a preliminary survey of the study area, and on 24 March and 2 April 1976; 2 medium-sized juveniles (approximately 2/3 adult diameter) were found on 5 May 1976; and 7 recently hatched young with remnants of the egg clutch were found on 16 July 1976. In addition, a copulating pair of snails was seen in the field in late February 1976. In the laboratory, snails collected in March 1975 began laying eggs in early June 1975 and ceased in early October. These snails again laid eggs from mid-February through June 1976.

Precopulatory behavior was not observed in the laboratory, although individuals with a swollen genital aperture were frequently seen. Only 1 pair of snails was discovered mating in the laboratory; they remained in coitus for at least 6 minutes before separating. Facing each other, the snails were positioned so genital apertures were opposed. Because detection of mating snails was rare, quantitative data on the interval between copulation and egg laying and on the number of clutches per copulation was not obtained. In that 1 case, which appeared to be a reciprocal copulation, 1 member of the pair laid 1 clutch of 96 eggs 7 days after mating. The other member of the pair, which had previously laid 2 clutches, laid no more eggs for the remainder of the season.

During the 1975 reproductive season, only 12 of the 21 adults deposited eggs. During the 1976 season, only 14 adults oviposited; 5 of these 14 adults had also laid eggs during the previous year.

The eggs were buried in moist soil or soft, rotting wood or deposited under the wet paper toweling. Most clutches were laid between late afternoon and early morning, but oviposition during the day was not uncommon. While laying eggs, the adult remained stationary with foot compacted and tentacles completely retracted; the anterior half of the body was usually obscured by the substrate in which the eggs were deposited. In 1 instance, an individual was observed laying eggs while upside down beneath the paper toweling. Since individuals were generally discovered already in the process of egg laying, information on the times required to deposit clutches of various sizes is not complete. However, the entire process required several hours; 1 individual was observed to take almost 19 hours to release a clutch. The position of ovipositing individuals prevented determination of time intervals between consecutively laid eggs. The number of eggs per clutch ranged from 43-105, with an average of 62.3 ± 18.2 (N = 61 clutches). Individuals commonly laid more than 1 clutch per season (average of 2.3, and range of 1-5). The interval between consecutively laid clutches from 1 individual ranged from 4 to 77 days. Table 1 summarizes the information on clutches obtained during this study. Fig. 1 shows the frequency of occurrence of different clutch sizes.

Destruction of eggs in freshly laid clutches by other adult snails was uncommon. Only 1 pair of adults consistently ate or broke each other's eggs once the laying process was completed; 5 of their 12 clutches were at least partially destroyed.

The eggs, containing an opaque-white, albuminous substance within a nearly transparent, colorless membrane, ranged in shape from distinctly elliptical to spherical, and averaged 4.70 ± 0.22 mm by 4.28 ± 0.17 mm in size (Table 1). Freshly laid eggs were somewhat flaccid and had a concave depression. Within approximately 2-4 hours after laying, the eggs were turgid, apparently having absorbed water from the soil, wood or paper toweling substrate. The eggs of a clutch were usually laid individually and were not attached to each other in the form of a string or enclosed in a common gelatinous mass. However, it was not uncommon for 2 eggs to be connected by a short, narrow, fragile pedicle or for 2 eggs to be enclosed within a common membrane.

TABLE 1. Egg clutch and hatchling data on *Triodopsis albolabris major*, arranged according to separate reproductive seasons, and also shown as composite values. The latter values are those cited in the text, unless stated otherwise.

Parameters measured	1975	1976	1975 and 1976 combined
$\bar{x}$ adult shell diameter	36.7 ± 1.5	36.7 ± 1.5	36.7 ± 1.5
$\bar{x}$ no. clutches per adult	2.2	2.5	2.3
no. eggs per clutch			
$\bar{x}$	63.3 ± 12.6	61.2 ± 16.5	62.3 ± 18.2
R	43 - 96	47 - 105	43 - 105
$\bar{x}$ egg diameter	4.40 ± 0.24	4.16 ± 0.27	4.28 ± 0.17
$\bar{x}$ egg length	4.85 ± 0.40	4.54 ± 0.32	4.70 ± 0.22
$\bar{x}$ development time (days)	21.8	20.5	21.2
$\bar{x}$ shell size at hatching			
diameter (mm)	4.03 ± 0.22	3.87 ± 0.39	3.95 ± 0.11
length (mm)	2.87 ± 0.13	2.85 ± 0.18	2.86 ± 0.01

R = range; $\bar{x}$ = mean; ± = standard deviation.

In the laboratory, the duration of development ranged from 18-24 days at 22°C, with an average of 21.2 ± 1.4 days. The percentage of eggs which hatched in each of the clutches maintained on wet paper toweling ranged from 0% to 81.8%, averaging 45.2%. Overall, 93.3% of the 1522 eggs produced during the 1975 season hatched. For clutches allowed to develop undisturbed in the soil, the number of eggs that hatched was much lower, with only 3-5 young emerging from large clutches of an undetermined number of eggs. It was not determined whether fungi, mites and/or enchytraeid worms, all of which were abundant in the soil around the clutch, on the eggs and inside some of the egg capsules, killed the developing embryos or the eggs were initially inviable. Few embryonic shells were found among the clutch remnants after hatching occurred.

The young snails hatched by eating their way out of the egg. The shadow of the developing young within the egg could be seen after about 16 days of incubation. Prior to this time, it was not possible to determine which eggs were viable and which were not. Eggs joined together by a pedicle or sharing a common membrane were not necessarily inviable. The hatchlings remained aggregated around the egg remnants for approximately 1 week; during that time, they ate the remnants of the hatched eggs and also the unhatched eggs (containing undeveloped or inviable embryos). The young aggregated and refused all vegetable foods regardless of whether or not they were allowed to remain with the egg mass. After 1 week, the aggregation dispersed, and the young readily consumed the previously mentioned foods. Shells of 630 newly hatched young had a narrow, deep umbilicus (with an umbilical diameter roughly 1/9 that of the shell), had 1 3/4 to 2 whorls, and averaged 4.03 ± 0.22 mm in diameter and 2.87 ± 0.12 mm in length (Table 1). The diameter of newly hatched young was roughly 1/10 that of the adults.

At hatching, the shells were a light amber-beige color, were very thin and fragile, and were nearly transparent. The mantle and organs of the visceral mass were easily seen. The digestive

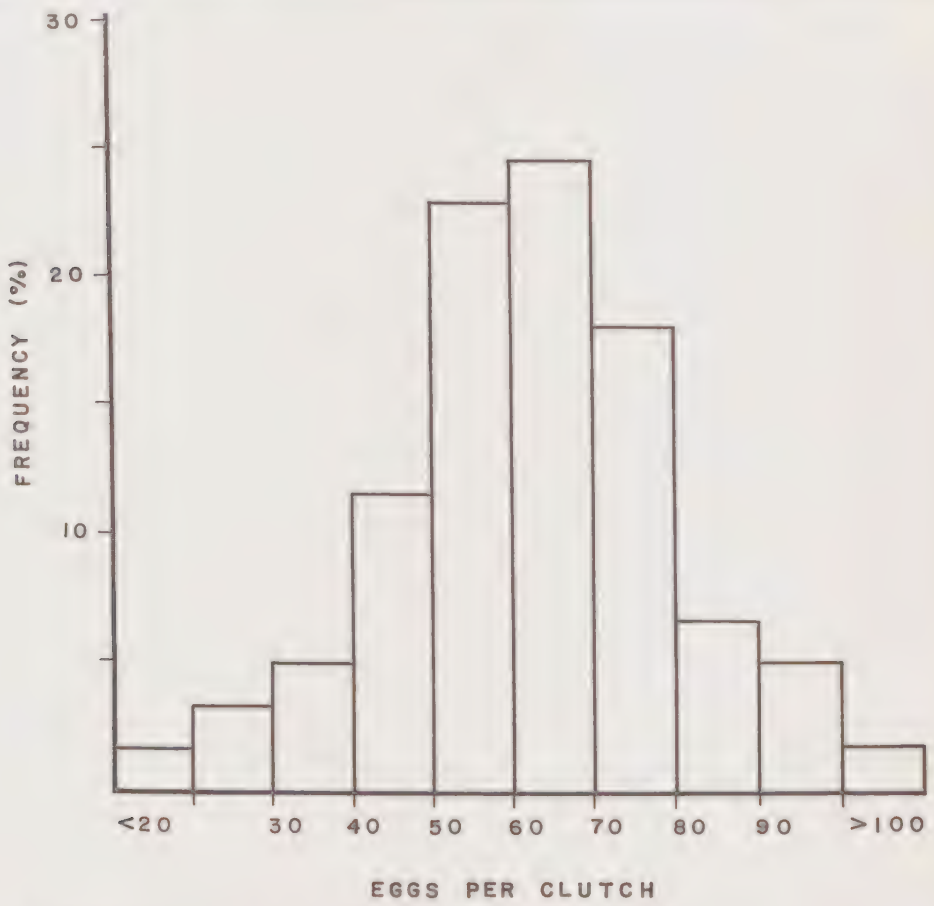

FIG. 1. Frequency histogram (% of sample) of *Triodopsis albolabris major* egg clutches of varying sizes. The frequencies are based on clutches from the 1975 and 1976 reproductive seasons.

gland in recently hatched young ranged from bright to light golden yellow in color; the columellar muscle and kidney were white, the heart a light translucent beige and the mantle beige with irregularly sized and spaced blotches of light black pigment. The head and foot were light gray to beige, the ocular tentacles a darker gray, and the eyes black. Within a week after hatching, the black blotches on the mantle had become darker, and, in general, the shell, head, foot and digestive gland colors darkened with age. The intensity of black on the mantle was variable in the young, even among those from the same clutch. In 1 clutch, 10 of 28 young which hatched lacked black pigment; in those young, the mantle, head and foot were whitish to light beige.

Growth in the young snails was initially rapid (see Fig. 1). The average increase in shell diameter per month per clutch for the 1st 6 months was 2.82 mm (N = 10 clutches). Growth rates declined as the age and size increased; the average increase in diameter per month per clutch during the 2nd 6 months was 1.56 mm. Individual growth rates were highly variable. Fig. 2 shows average growth rates of the young in 5 different clutches; Table 2 shows growth rates for individual young specimens from the same clutch from the age of 8 through 52 weeks (individuals less than 8 weeks were too small and fragile to mark). The ratio of shell length (L) to shell diameter (D) decreased with age. The average L/D ratio in 194 newly hatched young from 5 different clutches was 0.70 (range: 0.55-0.84). At 6 months of age, the average L/D was 0.60 (range: 0.56-0.64; 125 young). At 1 year, the average was 0.58 (range: 0.51-0.66 for 64 young).

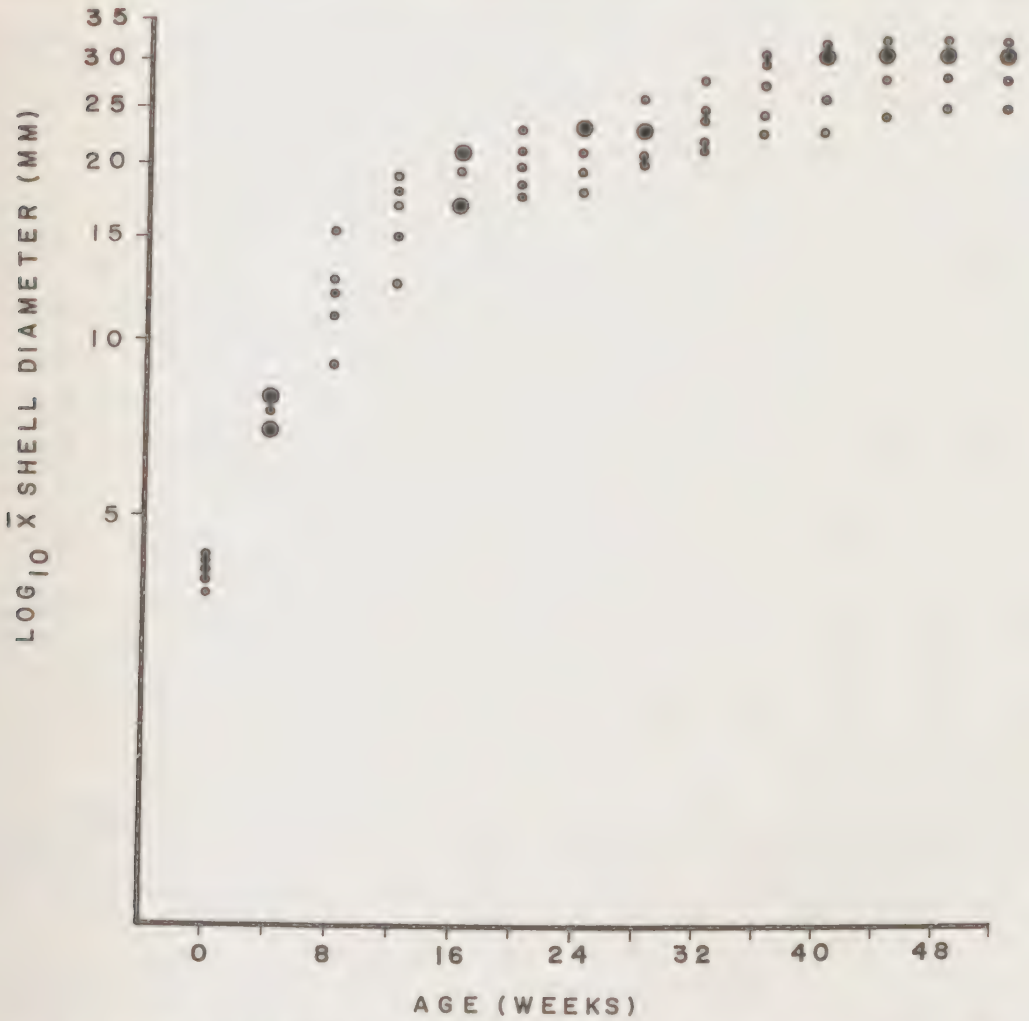

FIG. 2. Average growth rates of *Triodopsis albolabris major* hatchlings from 5 clutches. The larger dots indicate that 2 clutches had approximately the same average shell diameter.

The reflected outer lip on the aperture, signifying the definitive shell form and the attainment of the individual's maximum size, usually formed after about 44 weeks. However, the reflected lip formed on some individuals that were only 36 weeks old and on others only after 48-52 weeks. The reflected lip was preceded by a distinct downward slant in growth of the body whorl, which was first noted in individuals as young as 32 weeks, but was more common at the age of 40 weeks. Regardless of age, the definitive shell form was not seen on any individual less than 30.0 mm in diameter and rarely on specimens less than 32.0 mm in diameter. Formation of the reflected lip proceeded in a ventral to dorsal direction, and, as it formed, the umbilicus was covered over. Once the definitive shell form was attained and growth had ceased, the shell seemed to become thicker, sturdier and completely opaque. In general, the adult size of laboratory-raised snails was smaller than that of field-raised snails. This was most likely a result of crowding.

The density of young in a container had a distinct effect on the growth rate. The greater the density, the slower the individuals grew and the greater the variability in growth rates among members of the clutch. For example, 3 young kept in a 14.0 x 10.0 x 4.5 cm plastic box measured only 21.0, 19.5 and 17.5 mm in diameter at the age of 9 months, a distinct contrast to the growth rates shown in Fig. 2 and Table 2. Not all members of a clutch attained

TABLE 2. Increase in shell diameter (mm) of sibling snails from the same clutch. Average diameter of the 31 young in the clutch at hatching was 4.12 mm. An asterisk denotes presence of reflected lip on the aperture.

Snail No.	Age (weeks)											
	8	12	16	20	24	28	32	36	40	44	48	52
2	9.9	15.1	18.2	21.2	22.5	–	24.0	27.5	31.2	32.7	32.8*	32.8*
3	15.2	20.6	23.7	23.9	23.9	–	24.6	27.6	30.8	31.9	32.5	32.8*
4	11.0	17.3	21.4	22.6	22.7	–	23.9	28.0	31.4	32.3	32.3	32.4*
16	14.7	20.3	22.8	23.7	23.7	–	24.5	29.3	34.3	34.3	34.3*	34.3*
18	12.8	19.2	23.6	24.3	24.3	–	24.5	28.4	33.1	33.1	33.7	33.7*
22	15.1	23.3	25.8	25.8	25.8	–	25.9	30.4	35.6	35.6	35.7*	35.7*
23	13.4	19.8	23.0	24.6	24.9	–	26.0	26.9	34.0	34.3	34.4*	34.4*
26	12.2	19.3	22.7	22.8	22.8	–	23.2	26.4	31.2	31.8	32.0	32.1
28	8.9	16.1	19.3	21.4	21.4	–	21.9	25.8	28.2	28.9	30.2	30.3
31	9.6	14.5	17.7	19.5	20.0	–	21.9	25.0	26.5	27.0	27.8	28.3

the definitive shell form or adult size within 52 weeks, and the higher the density the more obvious and debilitating the stunting of individuals. There were indications that a high density might exert a more suppressive effect on growth in very young snails than on older juveniles previously raised at lower densities. Unfortunately, neither time nor facilities were available to pursue these preliminary observations on density effects.

Young maintained at higher densities appeared to be more aggressive toward each other as suggested by the damaged and scarred shells of some individuals. It was not unusual to observe 1 snail "chewing" on the shell of another. Damage to the victim's shell ranged from merely a jagged margin of the aperture (which could be repaired, but produced a stunted, scarred shell) to complete removal of the body whorl. The ultimate expression of aggression was cannibalism. There seemed to be no criteria for predicting which individuals would be cannibalized; they were not always the smaller or more lethargic members of the clutch, nor were they always the ones with heavily scarred shells. Cannibalism always occurred via the aperture; in no case was the victim consumed through a hole chewed in the apical area of the shell. By the age of 6 months, cannibalism, but not shell chewing, had ceased.

Young that hatched in 1975 matured and laid eggs within 1 year. Average clutch size for the 1st reproduction in the laboratory-raised animals was 46.13 ± 20.56 eggs (range: 17-99), as compared to 62.3 in animals from the field. Whether or not the smaller clutch size was effected by a smaller adult size or by laboratory conditions, or by both, could not be determined. Also, 1 of these animals laid 7 clutches during the 1 reproductive season, far more than any of the older snails. Egg size and hatching time did not seem to differ greatly from that observed in clutches from the older animals.

DISCUSSION

Comparison of reproduction in *Triodopsis albolabris major* to that in other congeners is difficult because few species have been studied, and for those species that have been observed

TABLE 3. Summary of previous observations on the eggs of *Triodopsis*.

Species	Egg size (mm)	No. eggs per clutch	Time of development (days)	Author
T. albolabris	–	–	21	Simpson (1901)
T. albolabris	2.3	15-20	–	Gugler (1963)
T. albolabris	–	–	14+	Kingston (1966)
T. dentifera	3.5	33	–	Ingram (1944)
T. multilineata	–	3-17	24-56	Kingston (1966)
T. tridentata	2.1	6	–	Ingram (1944)
T. tridentata	–	–	–	Kingston (1966)

the information is incomplete and not readily comparable. Table 3 summarizes data from previous studies. Whether the larger egg size and greater number of eggs per clutch in *T. a. major* is an effect of larger parental body size cannot yet be stated. Although adult shell sizes were not given in the previous studies and adult size ranges stated by Pilsbry (1940) and Burch (1962) indicate *T. a. major* to be the largest *Triodopsis*, laboratory conditions encountered by the other taxa could have been less than optimal for reproduction. Simpson (1901) reported *T. albolabris* to lay eggs year round in the laboratory, but gave no data on egg or clutch sizes. On the other hand, Ingram's (1944) observations on clutch size in *T. dentifera* were based on eggs from 1 individual that he found laying eggs in the woods and took back to the laboratory, where more eggs were laid later that day. In other studies the number of adults and clutches examined was not stated.

Observations on the young of *Triodopsis* are even more scarce than information on eggs. Cannibalism was reported in *T. albolabris* by Simpson (1901), who attributed it to an inadequate food supply. In my study, cannibalism was frequently seen despite an abundance of food. It seemed to be an effect of higher densities. The aggregation behavior of the young and their utilization of the eggs as the 1st source of food have not been mentioned previously.

The laboratory observations on egg size, number of eggs per clutch, clutches per individual and the aggregation behavior of the young are most likely similar to what is occurring under natural conditions. However, the duration of the breeding season under natural conditions could be quite different from that observed in the laboratory. For each of the 2 years of this study, the laboratory animals oviposited only during a 5-month period, not year-round. However, the 2nd reproductive period began in mid-February; the 1st reproductive period was in June. This earlier initiation of the breeding season could have been the result of a continuous warm temperature (22±°C). In any event, the reproductive period observed in this study was considerably longer than those reported for *Triodopsis albolabris* by Gugler (1963) and Kingston (1966): 1 and 2 months, respectively. A reproductive season similar to that seen here was recorded by Kingston (1966) for *T. multilineata*: oviposition from January through May.

In the field, adult snails probably oviposit each year. During this laboratory study, only 5 of 21 adults oviposited during 2 consecutive reproductive seasons. It is possible that the density of snails in the aquaria inhibited the reproductive patterns of some individuals, although this was not confirmed. A study using "wild" specimens is now underway to determine any seasonal reproductive patterns. This will, hopefully, clarify the laboratory observations.

The number of young to hatch from a clutch of eggs under field conditions is probably quite variable and much lower than what was observed in the laboratory. By incubating eggs

on paper toweling, problems with enchytraeid worms, mites and fungi were minimized and many eggs hatched. In contrast, as previously mentioned, eggs left to incubate undisturbed in soil produced very few young. The soil conditions in the laboratory were most favorable for worms, mites and fungi, and large numbers of them accumulated around the rotting vegetable material and the egg clutches. In the field these organisms may not be quite so abundant and thus cause less damage to the incubating egg clutches. Whether or not there were other predators on the eggs was not determined, since eggs were not found in the field. Ingram (1944) reported the short-tailed shrew to be a predator on the eggs of *Triodopsis albolabris* (he did not state whether adult snails were also preyed upon).

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ECOLOGICAL FACTORS INDUCING ESTIVATION IN THE FRESHWATER LIMPET *FERRISSIA WAUTIERI* (BASOMMATOPHORA: ANCYLIDAE). III. DENSITY LEVELS AND FOOD SUPPLY. GENERAL CONCLUSIONS

Monique Richardot

ABSTRACT

The effects of limpet density levels in inducing estivation and septum formation were studied. In all cases, high density levels played a positive role. The effects of starvation followed by food on the development of limpets at different stages were also investigated. In some cases, the septum was formed during starvation, but such a process likely can occur *in spite* of starvation. A new supply of food may initiate septum formation in ancyloids, whereas it does not always trigger a resumption of growth in septifers. These experiments provided evidence about the striking instability of the septifer stage.

A record of the best laboratory rearing method for obtaining septifers and post-septifers, of *Ferrissia wautieri*, is presented, as well as an insight into some of the physiological mechanisms involved in initiating estivation and a comparison of estivation in *Ferrissia wautieri* with that found in other mollusks.

INTRODUCTION

It has been established that the septifer form in *Ferrissia wautieri* is a drought resistant form (Richardot, 1974, 1976). In previous papers, the effect of various ecological factors on the initiation of septum development in *Ferrissia wautieri* was examined – the effect of oxygen content, organic matter content and pH of the water in the initial paper (Richardot, 1977a), and the influence of photoperiod, light intensity and water temperature in the 2nd article (Richardot, 1977b). The present study was carried out to establish the role played by density levels and experimental starvation on the initiation of the estivation form (the septifer stage). In spite of a population concentration linked to a decrease in water level, these factors (density and starvation) probably do not play a role in the natural habitat, but it was thought important to determine their role under experimental conditions.

METHODS

The experimental rearings were conducted in climatic rooms. The water temperature was 25°C, the photoperiod was 16 hours light, and the spatial variation in light intensity was 600-900 lux. The limpets had been bred according to methods C or E of Richardot (1977b). In each experiment the limpets came from the same strain. In method C, 40 newly hatched juveniles were immersed in 250 ml of water with a piece of a *Typha* leaf in a 375 ml jar. The water and *Typha* were collected in the natural habitat of the limpets. The jars were covered with a transparent plastic sheet, food was distributed at weekly intervals, and all jars of an experimental group received an equal part of the same *Typha* leaf. The water was never replaced.

In method E, the newly hatched juveniles were immersed in water previously loaded with organic substances. In each jar (45 ml), 5 newly hatched juveniles were immersed in 15 ml water with a piece of a *Typha* leaf. Equal parts of the same *Typha* leaf were distributed in the jars of an experimental group at weekly intervals. The oldest piece of *Typha* was removed, so that throughout the experimental period (except the 1st week) each jar contained 2 pieces of *Typha* leaf.

Septifer percentages obtained with rearing method C were calculated with regard to the total number

of living limpets which were 1.29 mm long or more (1.29 mm is the shell length of the smallest septifer obtained in the laboratory or collected in the natural habitat throughout a 10-year period). The septifer percentages obtained were analysed by non-parametric tests (Siegel, 1956), i.e., the Mann-Whitney U test and the Kruskal-Wallis H test. Shell lengths were measured by means of an ocular micrometer.

RESULTS

Density level

The study concerning effects of density levels and density variations was carried out in 2 different ways: 1) by a comparison of groups at a similar density in different volumes of water; and 2) by a comparison of groups at different densities in similar volumes of water.

Comparison of groups at similar density in different volumes of water (Experiment 1)

A series of 4 sub-experiments were performed at the same time, using breeding method C. Each experiment used 120 newly hatched limpets from the same strain, which were divided into 3 groups of 40 specimens each. One group was kept in 100 ml of water, the 2nd group in 150 ml of water, and the 3rd group in 250 ml of water. The jars were provided weekly with a similar surface of the same *Typha* leaf.

The total numbers of limpets recorded 6 weeks after the start of the experiment (Table 1) and the shell length of these animals show that only some limpets belonging to the 2nd generation had just hatched. Therefore, the septifers belonged to the 1st generation.

The septifer percentages were significantly different ($H=5.11$, significance for $P=0.05$) in the 3 volumes of water. The difference between septifer percentages obtained in 100 ml and in 250 ml is highly significant ($U=0$, significance for $P=0.01$).

Four weeks later (Table 1), the 2nd generation subjects were present everywhere, except in the 2 jars where the total population was estivating; some of the limpets had reached the critical phase of their development in 250 ml jars, and the septifers may be of the 2nd generation. The septifer percentages were increasing everywhere, but the differences between them were no longer significant.

The data show clearly that, in a confined space, the growth of the limpets and their reproductive activity are obviously affected. These confined conditions are more favorable for septum formation than a large living space. But this holds only throughout a first period. Low density levels (i.e., in the jars containing 250 ml of water) at the start of the experiment resulted in a short-term increase in density (rapid growth rate and good reproductive activity), so that 6 weeks after the start the septifer percentages were low. But, later, as the space becomes more and more confined and 10 weeks after the start of the experiment, the number septifers is increasing. So, the phenomenon is only delayed.

Comparison of groups at different densities in similar volumes of water

Experiment performed according to the rearing method C (Experiment 2)

At the start of the experiment, the 240 newly hatched limpets of different strains were randomly divided as follows: 4 jars had 10 limpets each (G10); 2 jars had 20 limpets each (G20); 2 jars had 40 limpets each (G40); 1 jar had 80 limpets (G80). For each food supply, at weekly intervals, equal parts of the same *Typha* leaf were provided, without taking density into account. After a 1st experimental period (6 weeks or 9 weeks), 3 counter-experiments were performed to provide information on the effect of decrease in density on the development of young limpets and septifers.

Three weeks after the start of Experiment 2 (Table 2), the highest septifer percentages occurred in jars G40. The growth rate of the limpets in jars G10 had been rapid. So, 19 limpets out of a total of 31 surviving individuals were mature. Eggs were numerous, and some limpets of the 2nd generation hatched. There were only 9 adults in jars G20, 6 in jars G40, and only 3 in jar G80.

TABLE 1. Effect of density levels on initiating septum development. Comparison of groups at similar density in different volumes of water. Rearing method C.

Jar	W	I	E	No. of ancyloids			S	No. of ancyloids s + m & S	%
				j	s	m			
6th week									
V1	100	32		2	8		22	30	73.3
V2	100	34		1	12		21	33	63.6
V3	100	36		1	15		20	35	57.1
V4	100	32			12		20	32	62.5
V5	150	46	22	5	12	2	13	27	48.1
V6	150	28			7		21	28	75.0
V7	150	43	17	2	13	1	23	37	62.1
V8	150	37	25		28		6	34	17.6
V9	250	50	69		15	8	8	31	25.8
V10	250	36	13	1	18	2	13	33	39.3
V11	250	38	22	1	22	3	9	34	26.4
V12	250	44	19	1	26	2	7	35	20.0
10th week									
V1	100	30					30	30	100.0
V2	100	46	41	13	6		27	33	81.8
V3	100	54	73	21	7		26	33	78.7
V4	100	42	133	9	13		20	33	60.6
V5	150	159	107	125	13	2	19	34	55.8
V6	150	26					26	26	100.0
V7	150	48	40	9	7	2	30	39	76.9
V8	150	62	64	26	13	2	21	36	58.3
V9	250	174	219	131	12	9	22	43	51.1
V10	250	160	106	110	12	7	31	50	62.0
V11	250	103	219	48	15	9	31	55	56.3
V12	250	81	46	32	14	2	33	49	67.3

W, water volume ml; I, total number of individuals; E, total number of eggs; J, juveniles which were less than 1.29 mm long; s, submature individuals which were less than 2.58 mm long; m, mature individuals which were more than 2.58 mm long; S, number of septifers; %, septifer percentage.

TABLE 2. Effect of density levels on initiating septum development. Comparison of groups at different densities in similar volume of water. Rearing method C.

Jar	J	I	E	No. of ancyloids			S	No. of ancyloids s + m & S	%	Med %
				j	s	m				
3rd week										
$G10_1$	10	5			3	1		4	0	
$G10_2$	10	10	24		6	3	1	10	10.0	3.3
$G10_3$	10	15	109	7	1	7		8	0	
$G10_4$	10	25	132	17		8		8	0	
$G20_1$	20	55	80	37	10	6	1	17	5.8	3.0
$G20_2$	20	17	7		14	3		17	0	
$G40_1$	40	36	17	1	16	2	13	31	41.9	35.0
$G40_2$	40	30	11		15	4	7	26	26.9	
$G80_1$	80	56	16		24	3	3	30	10.0	
6th week										
$G10_1$	10	24	60	19	1	3	1	5	20.0	
$G10_2$	10	41	53	32	1	5	4	10	40.0	18.1
$G10_3$	10	145	104	137	2	7	1	10	12.5	
$G10_4$	10	176	109	169	5	7		12	0	
$G20_1$	20	105	67	87	2	7	9	18	50.0	55.5
$G20_2$	20	36	46	18	4	3	11	18	61.1	
$G40_1$	40	53	42	23	14	3	13	30	43.3	52.6
$G40_2$	40	41	91	12	7	4	18	29	62.0	
$G80_1$	80	57	48	17	17	3	17	37	45.9	

J, number of juveniles at the start of experiment; I, total number of individuals; E, total number of eggs; j, juveniles which were less than 1.29 mm long; s, submature individuals which were less than 2.58 mm long; m, mature individuals which were more than 2.58 mm long; S, number of septifers; %, septifer percentage; Med %, median septifer percentage.

Three weeks later the septifer numbers were increasing in all jars, but septifer percentages were higher in jars that had a high density of limpets at the start of the experiment (G20, G40, G80). The differences were significant with the test of Kruskal-Wallis (for P=0.03), the data of G80 being ommitted. In all cases, as the number of septifers increased, the number of adults became steady. Besides, the lower the initial density level, the higher the number of limpets in the 2nd generation, but the growth of young animals nearly came to a standstill and the septifers present were probably from the 1st generation.

At the end of this 1st experimental period (6 weeks), 105 limpets were removed from jar $G10_3$, leaving 40 young limpets in this jar. They were all less than 0.86 mm in shell length. Five weeks later, the 34 surviving animals were estivating.

Meanwhile, the population of $G10_4$ was kept without change. Three weeks later (9th week), no septum formation was observed. The growth rate of the young limpets was very slow and their shells were very dark. Then 135 limpets were removed and only 20 young (<0.86 mm) individuals were kept in this jar. Four weeks later 3 limpets died, 2 had reached sexual maturity as ancyloids and 15 were estivating.

In order to observe the effect of a decrease in density on the estivating limpets, another experiment was carried out. After the 1st experimental period (6 weeks), all the ancyloids were removed from jars $G20_1$ and G80: 20 septifers were kept in each jar. Four weeks later a very slight new growth of shell could be observed in only 1 septifer, which died some days later.

Experiments performed according to rearing method E (Experiments 3 and 4)

For each experiment, 25 limpets were divided into 5 groups of 5 specimens, and 25 other limpets were isolated (1 limpet per jar). At the end of Experiment 3, 18 limpets out of a total of 20 surviving individuals reared in groups were estivating, whereas only 6 septifers could be observed out of a total of 23 surviving individuals in jars which contained only 1 limpet (Table 3). In Experiment 4, the difference between septum formation in limpets reared in groups and isolated was less significant: 13 out of 18, and 5 out of 18, respectively (Table 4).

In Experiment 3, the growth of the limpets reared in groups was slower than growth of isolated individuals, but in Experiment 4 it was not so obvious.

The data from these series of density experiments provide strong arguments that high density levels play a role in septum formation under laboratory conditions. However, the set-up of these experiments implied large differences in available food, the *Typha* leaf surface provided being similar regardless of the limpet density. Therefore, further studies were needed to show the interactions between food and density.

On the basis of these data, it could be inferred, at first sight, that, as has been found in other mollusks, high density levels affect reproductive activity. In submature *Ferrissia*, the limpets would form a septum if the oviposition was inhibited. But, such an assumption regarding reproductive activity cannot account for the high septifer percentages obtained after a decrease in density (i.e., as found in the counter experiment). Moreover, a decrease in density level was not sufficient to terminate estivation in septifers.

It appears that high density levels may have an indirect effect on the initiation of estivation, because such levels may promote septum formation by slowing down the young limpets' growth rates.

It is now known that, in experiments carried out according to rearing method C, the water qualities become progressively worse so that, when the oxygen content of the water is low and the organic matter high, environmental conditions are not favorable and submature limpets form a septum. Moreover, it can be assumed that high densities result in a slowing down of the limpets' growth rates[1]. Therefore, the higher the density level, the slower the growth

[1] The inhibition of growth of mollusks under over-crowded conditions has been observed by several authors (e.g., Wright, 1960; Shiff, 1964; Seed, 1968; Struhsaker & Costlow, 1969; Mooij-Vogelaar et al., 1970, 1973; Mooij-Vogelaar & van der Steen, 1973; etc.).

TABLE 3. Effect of density levels on initiating septum development. Comparison of groups at different densities in similar volumes of water. Rearing method E.

Jar	2nd week		3rd week		4th week		5th week	
	Size[1] (mm)	S or A	Size[1] (mm)	S or A	Size (mm)	S or A	Size (mm)	S or A
V1	2.15		2.49	S	2.58	S		
V2	2.28		2.67	A				
V3	died							
V4	2.62		2.62	A				
V5	2.45		3.01	A				
V6	2.15		2.36	S	2.36	S	2.45	S
V7	2.79	A						
V8	2.71	A						
V9	2.06	S	2.32	S	2.36	S		
V10	2.49	A						
V11	2.58	A						
V12	2.24	S	2.36	S	2.41	S		
V13	2.49		died					
V14	2.11		2.41	S	2.54	S		
V15	2.67	A						
V16	1.63		2.79	A				
V17	2.32		2.67	A				
V18	2.49	S	2.49	S				
V19	2.58		3.01	A				
V20	2.24	S	2.84	A				
V21	2.54	A						
V22	2.32		2.75	A				
V23	2.36		3.27	A				
V24	2.75	A						
V25	2.15		2.58	S	2.75	S	2.75	S

Jar	2nd week			3rd week			4th week			5th week		
	I	Med[2]	s	I	Med[2]	s	I	Med[2]	s	I	Med[2]	s
R1	5	1.33		5	1.55	1	4	1.89	1	4	2.32	3
R2	4	1.59		4	1.98	2	4	2.19	3	4	2.28	4
R3	4	1.42		4	1.68	1	4	1.98	2	4	2.24	4
R4	4	1.85		4	2.11	4	4	2.24	4	4	2.28	4
R5	5	1.46		4	2.06	1	4	2.36	3	4	2.54	3

V, isolated limpets; R, groups of 5 limpets; A, indicates that the limpet was ancyloid and the 1st egg-laying had occurred; S, indicates that the limpet was a subseptifer or a septifer; s, septifer; I, number of individuals; Med, median size (mm).

[1] Median size for all of the individuals in all of the jars at the end of the 2nd week = 2.28 mm, the 3rd week = 2.67 mm.

[2] Median size in mm for the individuals in each jar. The median size for the total number of individuals in jars R1, R2, R3, R4 and R5 at the end of the 2nd week = 1.50 mm, the 3rd week = 1.85 mm, the 4th week = 2.15 mm, the 5th week = 2.32 mm.

TABLE 4. Effect of density levels on initiating septum development. Comparison of groups of different densities in similar volumes of water. Rearing method E.

Jar	2nd week		3rd week		4th week		5th week		6th week		7th week	
	Size[1] (mm)	S or A	Size[1] (mm)	S or A	Size[1] (mm)	S or A	Size (mm)	S or A	Size (mm)	S or A	Size (mm)	S or A
N1	0.90		2.36		2.75	A						
N2	1.25		2.45		2.75	A						
N3	1.03		1.98		2.58	A						
N4	1.59		2.58	A								
N5	1.38		2.49	A								
N6	0.90		1.98		2.45	S	2.49	S				
N7	1.29		1.55		2.36	A						
N8	1.25		2.36		2.84	A						
N9	0.86		0.95		0.95		1.59		2.32	A		
N10	died											
N11	0.99		1.98		2.88	A						
N12	1.16		2.19		2.58	A						
N13	0.73		0.86		died							
N14	0.90		1.07		1.33		2.06	S	2.19	S	2.06	S
N15	1.20		2.41		2.92	A						
N16	0.90		1.16		1.89		2.02		2.15	S	2.06	S
N17	1.33		2.67		3.01	A						
N18	1.25		2.45		2.79	A						
N19	1.38		2.62	A								
N20	1.16		1.89		2.41	S	2.15	S				

Jar	2nd week			3rd week			4th week			5th week			6th week			7th week		
	I	Med[2]	s	I	Med[2]	s	I	Med[2]	s	I	Med[2]	s	I	Med[2]	s	I	Med	s
O1	5	1.38		5	1.68		4	1.76	2	4	1.85	2	4	2.02	3			
O2	4	1.33		4	1.93		4	2.06		4	2.06	2	4	2.15	2	4	2.15	2
O3	5	1.20		5	1.59		5	1.81	1	5	1.93	3	5	2.02	3	5	2.11	4
O4	5	1.33		5	1.93		5	2.02	3	5	2.02	4	5	2.11	5			

N, isolated limpets; O, groups of 5 limpets; A, indicates that the limpet was ancyloid and the 1st egg-laying had occurred; S, indicates that the limpet was a subseptifer or a septifer; s, septifer; I, number of individuals; Med, median size (mm).

[1] Median size for all of the individuals in all of the jars at the end of the 2nd week = 1.12 mm, the 3rd week = 2.02 mm, the 4th week = 2.45 mm.

[2] Median size in mm for the individuals in each jar. The median size for the total number of individuals in jars O1, O2, O3 and O4 at the end of the 2nd week = 1.33 mm, the 3rd week = 1.76 mm, the 4th week = 1.89 mm, the 5th week = 1.98 mm, the 6th week = 2.06 mm.

rate of the young limpets, and, when the limpets reach the critical phase in their development, the quality of the water is so bad that they form a septum.

In Experiment 2, the adult ancyloids were no more numerous after 6 weeks than 3 weeks previously. Only limpets which grow rapidly can reach sexual maturity before the water becomes badly degraded. Six weeks after the start of the experiment, the density level was high and the growth rate of newly hatched individuals came nearly to a standstill. Then, a decrease in density (the counter experiment) resulted in a new start of growth, so that the young limpets approached sexual maturity. But, if the water quality was bad, the conditions were not favorable for reproductive activity, and the limpets then form a septum.

Food supply

The previous experiments showed that limpets can form a septum even though they had a food supply (*Typha* leaves covered with algae). Thus, starvation is not needed to initiate septum formation. However, it was of interest to investigate the consequences of a period of starvation followed by a new supply of food on the development of limpets at different stages.

In the initial experimental period, the limpets were bred according to method E, which allowed the development of each animal to be followed. As soon as 1 or more limpets in a jar showed the morphological characteristics of a subseptifer[2], or the first signs of septum development, all individuals in the jar were deprived of food. The pieces of *Typha* were removed and the limpets were kept in the jar without food for 3 or 4 weeks. During this period of starvation, the shell and septum growth rate decreased and stopped completely. Then the limpets were fed again. Four experiments were performed; 3 experiments used 50 limpets each and 1 experiment used 100 limpets.

Effect of starvation

The 5 newly hatched limpets in any one jar did not have the same growth rate throughout the 1st experimental period. So, when starvation occurred, some limpets were young ancyloids, others had the lateral borders of their shells slightly constricted inwards (they were at the subseptifer stage), and in other cases the limpets' septa were in a rudimentary state.

The results of the 4 experiments are recorded in Fig. 1. The 1st number (211) represents the total number of surviving limpets just before the starvation period. Among them (1st column of Fig. 1), there were 52 ancyloids (A), 59 subseptifers (SSa), 99 limpets with a septum in the process of being formed (SS), and 1 septifer (S).

During the starvation period, the ancyloids, if they survived, remained at this stage, their growth rate at first decreasing, then stopping completely (only 1 limpet had the subseptifer shell shape); some subseptifers died (represented by 6 + in Fig. 1) (among surviving specimens, several (23 SSa) remained at this stage, but septum formation was also possible, and even some animals completed it (16 S)); out of 99 limpets with a rudimentary septum, most completed the calcareous layer and reached the septifer stage (91 S) during the starvation period.

Effect of new weekly food supplies

After the starvation period, 165 limpets (40 ancyloids, 24 subseptifers, 19 limpets with an incomplete septum and 82 septifers) were fed again. Some ancyloid limpets died (10 + in Fig. 1). Among surviving limpets, the new food supply triggered off either a resumption of shell growth (25 A) (hence reproductive activity) or septum formation (3 + 2) (hence estivation (2 S)). The subseptifer individuals generally lost their morphological characteristics and finally followed the ancyloid course of development. However, some of them retained the

[2] In a subseptifer, the lateral borders of the anterior third of the shell become constricted inwards, while, anterior to this, certain longitudinal ribs thicken and become very obvious (Richardot, et al., 1972).

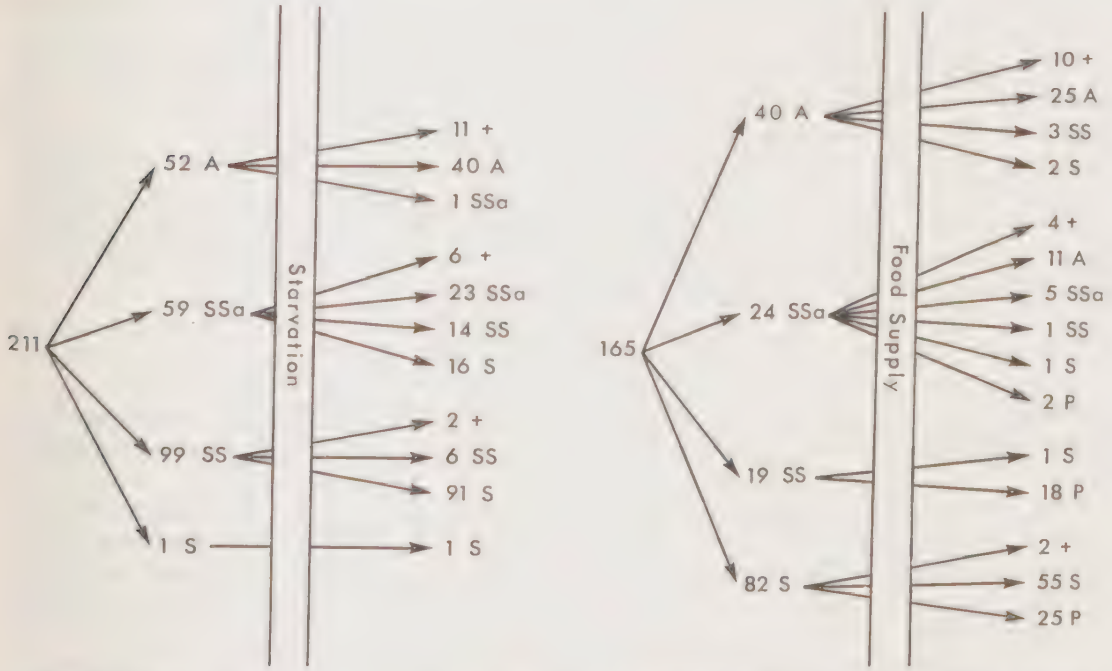

FIG. 1. Effect of a period of starvation followed by a new food supply on different stages of development of *Ferrissia*. A, ancyloid; SSa, subseptifer; SS, septum in course of formation; S, septifer; P, postseptifer.

subseptifer shell shape without any resumption of growth. In 4 cases, the new food supply initiated septum formation, but only 1 limpet reached the estivation stage; in 2 limpets, 2 weeks later, septum growth stopped, whereas shell growth started and the individuals reached reproductive maturity as postseptifers (P) with incomplete septa. Most of the limpets with an incomplete septum reached reproductive maturity. In only 1 individual did the resumption of growth involve the septum, ending in estivation. In 55 individuals (out of the total 82 septifers), estivation was not terminated by a new supply of food, whereas in 25 cases (P) a resumption of growth occurred.

It can be inferred from the results obtained in these experiments that starvation does not immediately stop the growth of the external calcareous sheathes (shell or septum). At first (for 2 or 3 weeks) growth may go on, probably as a result of tissue storage (Richardot & Wautier, 1972; Richardot, 1976). So, in ancyloids there is an increase in shell length, whereas in other limpets septum construction can be observed. But only those limpets whose septa were initiated before starvation can complete their septa.

Starvation is not to be understood as a factor that initiates septum formation. In some cases the septum is formed during the starvation period, but most likely such a process can occur *in spite* of starvation. Furthermore, the 2nd part of these experiments showed that a new supply of food may initiate septum formation in ancyloids, whereas it does not always trigger a resumption of growth in septifers.

Possibly the most important information provided by these experiments concerned the different levels of physiological stability in the ancyloid, subseptifer and septifer stages. The subseptifer stage is obviously the most unstable one. In subseptifers, starvation or feeding initiates a large number of different developmental paths. This may be related to the instability of this stage, which represents a critical period of development. It can be observed that only 1 ecological factor may result in several different consequences in the development of subseptifer limpets. For example, a new food supply after a period of starvation generally

initiates reproductive activity in these limpets; but then they may exhibit either an ancyloid shell shape or a postseptifer shape with an incomplete septum. In the 1st case, the new food supply initiated shell growth, whereas in the 2nd case it first initiated septum formation and then later shell growth (P). Thus, it would appear that the limpets were vacillating between 2 developmental ways: estivation or growth and then reproduction.

During septum formation, the direction of development is still reversible and resumption of growth and reproduction are easily initiated. But, the septifer stage is more stable; in this stage, the reversal of estivation is more difficult to obtain. However, it is noticeable that in one jar a new food supply initiated estivation in an ancyloid and reversed estivation in a septifer. Such an observation shows the complexity of this problem.

GENERAL CONCLUSIONS

The 1st conclusion to be drawn from the study on septum formation in *Ferrissia wautieri* was the significance of the septate form: the septifer is a drought resistant form (Richardot, 1974, 1976).

Possibly the most important contribution of this ecological study is the perfection of a simple rearing method to obtain, in the laboratory, either septifer or postseptifer limpets. This method consists of rearings conducted in a climatic room under summer-time conditions, i.e., high constant temperature (25°-30°C), long daylight (16 hours), and high light intensity (about 600-1000 lux). Fourteen or 15 newly hatched juveniles in 100-150 ml of water represent the most favorable population density level at the start of an experiment. The amount of food supplied weekly must be about 10-15 cm of *Typha* leaf (the limpets eat the algae which grows on the immersed part of the *Typha* leaves). To prevent evaporation and gaseous exchange, jars must be covered with a close-fitting transparent plastic sheet. Septifer percentages will be high if the juveniles are taken from strains freshly collected in the field and reared under summer-time conditions (Richardot, 1976). To obtain good reproductive activity, it is necessary to renew the water and *Typha* leaves at weekly intervals and to remove some individuals in order to avoid over-crowding. Maximum septifer percentages are obtained after 6, 8 or 10 weeks. The limpets can be brought out of estivation by renewing the water and the *Typha* leaves or, more efficiently, by placing 5-10 septifer limpets into a clean jar with 250 ml of water and 10 cm of a newly collected *Typha* leaf. Such an environmental renewal triggers a resumption of growth, the postseptifer stage is reached, and generally 1 week later the 1st egg laying takes place. Accordingly, we are now able to obtain septifers and postseptifers in the laboratory at will, and thereby *Ferrissia wautieri* becomes very suitable material for further ecological and physiological investigations concerning estivation.

In addition to providing a method of inducing estivation or reversing it, this ecological study throws light on some physiological mechanisms involved in the initiation of septum development. Juvenile growth can go on in bad environmental conditions, until the animal reaches the critical physiological state, which takes place just before sexual maturity. Then growth stops and the limpet develops a septum. Therefore, physiological requirements seem to change throughout development. This critical phase seems to be characterized by a hypersensibility of the organism to several environmental factors: high temperatures, an increase in organic matter in the water and, probably of most importance, anoxy. It would not be surprising to find a close correlation between gamete maturation and an improvement in ecological conditions. The role played by oxygen content of the water may be especially important. In *Ferrissia*, reproductive activity probably requires an increase in oxygen consumption, as has been found in *Ancylus fluviatilis* (Berg et al., 1958). Of particular relevance to the present discussion are the observations of van der Steen (1967) about the increase in egg-laying activity as a consequence of increasing water oxygen content (renewal of the water). Similar results also have been obtained in *Ferrissia*. Inagaki (1972) stated that in *Littorina saxatilis*, a decrease in the rate of sexual maturity was correlated with a decrease in respiratory rate.

If our presumptions are correct and confirmed by further investigations, the following mechanisms may be involved in the initiation of septum development. In summer time, when the mud is still covered by a thin water layer, but just before drought, the oxygen content of the water is decreasing (Richardot, 1974, 1976). At that time juvenile growth is not inhibited; they tolerate the poor water oxygen content. However, in submature limpets, since the increase in oxygen demand (required by sexual maturity) is not satisfied, the reproductive processes would stop and the initiation of septum development would occur.

On the basis of the data provided by my ecological studies, performed both in the natural habitat of *Ferrissia wautieri* and in the laboratory, it is now possible to compare estivation in *Ferrissia wautieri* with that in other mollusks. As observed in other estivating gastropods generally, estivation (the septifer stage in *Ferrissia wautieri*) is characterized by the reduction of the shell aperture and a slowing down of metabolism (Wautier & Badarelli-Mille, 1966; Wautier et al., 1966). Moreover, estivation in *Ferrissia wautieri* is initiated by a combination of several ecological factors (chemical quality of the water, high temperatures, long daylight); similar situations exist for other gastropods (Fischer, 1950; D. Bonavita, 1964; Abeloos, 1965; A. Bonavita, 1965; Pomeroy, 1968; Sturrock, 1970; Din, 1971; Gainer, 1972).

Nevertheless, the following arguments lead us to consider the estivation in *Ferrissia wautieri* as obviously original. (1) Septum development is not initiated by drought, but by the reduction in water level and by the accompanying chemical changes in the water which precede the drought. (2) The septum is a thin calcareous layer (the crystalline structure of which is similar to the shell; Richardot et al., 1972) and septum development is not immediate, but requires 8 or more days. (3) The septum remains; it is not removed when environmental conditions are favorable again. A definitive trace is left on the shell as a result of chemical changes accompanying receding water. Therefore, it is even possible to tell from a shell found with only a slight irregularity of the posterior surface (septum development interrupted; see Richardot et al., 1972; Richardot, 1976) that a reduction in water level occurred, even though it had not been followed by drought. (4) Only the submature individuals are able to develop a septum that can aid them in avoiding unfavorable environmental conditions. The production of this calcareous layer is linked to a precise physiological state which occurs just before sexual maturity. Deposition of the 1st batch of eggs completely prevents new septum formation no matter what environmental conditions the limpet may suffer subsequently. Therefore, this method of development provides only one possibility for each individual to initiate its breeding period once conditions become favorable again. Thus, it may represent a highly differentiated mechanism for species protection.

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THE SHELL SURFACE SCULPTURE OF *CARYCHIUM NANNODES*. – The Carychiidae in North America comprise several species with rather distinct shells and some nominal taxa with shells less distinctly differentiated. The recognizable forms in North America include the following nominal taxa: *Carychium clappi* Hubricht 1959, *C. exiguum* (Say 1822), *C. exile* H.C. Lea 1842, *C. exile canadense* Clapp 1906, *C. mexicanum* Pilsbry 1891 (including *C. floridanum* Clapp 1918), *C. nannodes* Clapp 1905, *C. occidentale* Pilsbry 1891, *C. riparium* Hubricht 1978 and *C. stygium* Call 1897. All of the nominal species and subspecies are based on characters of the shell; whether or not they all deserve taxon names is not yet settled. An additional species, the European *C. minimum*, was introduced into a greenhouse in Norfolk Downs, Quincy, Massachusetts (W.F. Clapp, 1912), but probably it did not become established.

Recently, we have been photographing the shells of North American carychiid species with the aid of a scanning electron microscope (SEM), an instrument that is especially useful in observing minute shells. We have observed that the surface sculpture of most of the North American carychiid species as seen with the SEM[(1)], although seen clearer, is basically the same as seen with the higher power objective of the stereoscopic dissecting light microscope. However, the surface of *Carychium nannodes* as seen with the SEM was strikingly different from the other species.

FIG. 1. Geo. H. Clapp's (1905) figures of *Carychium nannodes*. FIG. 2. Winslow's (1922) figures of *C.* sp. (= *C. nannodes*). FIG. 3. Geographic distribution of *C. nannodes*.

Carychium nannodes is the smallest species of Carychiidae occurring in North America, its shell measuring only 1.3 to 1.5 mm in length. It was described originally by G.H. Clapp (1905) from Monte Sano, about 5 miles east of Huntsville, Alabama. Clapp's illustrations of the shell are shown in Fig. 1 above. It has been found frequently since, but almost entirely in the southern Appalachian mountains, from West Virginia to northern Alabama (Fig. 3). Several isolated populations have been discovered beyond this area, in southwestern Michigan and southern Ontario. Clapp described the shell surface of *C. nannodes* as "differ[ing - from *C. exile*] in being absolutely smooth, *without any trace of growth lines*, even when magnified 60 diameters; under high magnification the surface shows a faint granulation." Further descriptions of the shell have been few, mostly limited to those of Winslow (1922) on the columellar folds. Winslow's figures are shown in Fig. 2 above.

The shell surface sculpture on *Carychium nannodes*, as seen with the SEM, consists of a series of parallel spiral rows of minute puncta (Fig. 5). On the 3rd whorl and the 4th (penultimate) whorls, these were counted. Here there are about 23-25 exposed spiral rows of puncta. The distance between spiral rows varies from about 0.005 to 0.025 mm, and the distance between individual puncta in a row varies from about 0.005 to about 0.02 mm. The shape of the puncta varies from round to oblong. Sometimes several puncta seem to coalesce, forming a short trough. Actually, these spiral rows of puncta can be seen under the ordinary steroscopic light microscope at magnifications as low as x20, but only if the shell surface is well cleaned and the proper illumination used. They cannot be seen as clearly with the light microscope as with the SEM, of course.

FIGS. 4, 5. SEM photographs of *Carychium nannodes* from Gurley, Madison County, Alabama, University of Michigan Museum of Zoology lot no. UMMZ 116227. FIG. 4. Shell of *C. nannodes*, x60. FIG. 5. Portion of the surface of the 3rd whorl of *C. nannodes*, x500. NOTE: *C. nannodes* from Toronto, Canada, has this same sculptured pattern.

Included in our observations were specimens from the type lot (UMMZ 33572). Although not studied with the SEM, the puncta can be seen clearly on these specimens with the light microscope.

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(1) The shells were cleaned for SEM observation by immersing them in a commercial laboratory glassware detergent and gently brushing with a fine brush. The shells were then carefully rinsed in several changes of distilled water, air dried, and affixed with copper conductive tape to the stub to be used in the SEM. Prior to study with the SEM, the shells were coated with gold.

A NOTE ON THE STATUS OF THE TYPE SPECIMENS OF *CONUS PRETIOSUS* AND *CONUS SEYCHELLENSIS* G. & H. NEVILL (GASTROPODA: CONIDAE).[1] – The type specimens of G. & H. Nevill's 2 species, *Conus pretiosus* and *C. seychellensis*, were neither properly designated nor figured. The status of the type specimens of both species are discussed below and the respective holotypes designated and figured for the first time.

G. & H. Nevill (1874) described as new 3 species of the genus *Conus* Linnaeus. None of these 3 species were figured. *Conus pretiosus* and *C. seychellensis* G. & H. Nevill were based on a single specimen each, collected from the Andaman and Seychelles islands respectively. The 3rd species, *C. masoni*, was known by 10 specimens (syntypes) collected from the Andamans.

Mr. William E. Old, Jr., of the American Museum of Natural History, New York, New York, U.S.A., requested a photograph of *Conus pretiosus*, if the type specimen of the species was available in the National Zoological Collections of the Zoological Survey of India. A search was initiated for the holotype of *C. pretiosus*, which was found in the general collection; the shell is now part of the Survey's type collections. The holotype of *C. seychellensis* was already in the type collections of the Zoological Survey, but all 10 syntypes of *C. masoni* are missing and all efforts to find them have failed. The 2 type specimens currently present in the Survey's collections are discussed more fully below, and illustrated.

Conus (Chelyconus) pretiosus G. & H. Nevill 1874, p 22, type locality, Andaman Islands. The "Register of Presentations to Indian Museum, Mollusca" has an entry against Register Number 2960 in the name of *Chelyconus pretiosus* Nevill, locality Andamans and dated 24-1-1894 (date of registration) for a single specimen (Fig. 1). However, there is no mention of the word "Type". The same data are repeated on the labels accompanying the specimen in the cardboard box. The description of the species given by G. & H. Nevill *(op. cit.)*, measurements and other collection data agree completely with the specimen. Moreover, it is pertinent to point out here that there are no other specimens of this species in the National Zoological Collections with this data. Therefore, the specimen No. 2960 in the Zoological Survey of India is hereby designated the Lectotype of *Conus (Chelyconus) pretiosus* G. & H. Nevill.

FIG. 1. *Conus (Chelyconus) pretiosus* G. & H. Nevill.

Conus (Rhizoconus) seychellensis G. & H. Nevill 1874, p 22-23, type locality, Seychelles Islands. In the "Register of Presentations to Indian Museum, Mollusca" there is an entry against Register Number 3028 for *Rhizoconus seychellensis* Nevill, locality Seychelles and dated 25-1-1894 (date of registration) for a single specimen (Fig. 2). The word "Type", however, is mentioned in this case and the same data are

also found on the labels in the cardboard box. The original description of the species agrees fully with the specimen. Therefore, this specimen is obviously the Holotype of *Conus (Rhizoconus) seychellensis* G. & H. Nevill.

FIG. 2. *Conus (Rhizoconus) seychellensis* G. & H. Nevill.

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THE U.S.S.R. ACADEMY OF SCIENCES
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MOLLUSCS
Their Systematics, Evolution and Significance

Abstracts of Communications
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PREFACE

These abstracts are from reports presented to the Fifth Meeting on the Investigation of Molluscs, which was organized by the Malacological Committee of the Scientific Council on "Biological Bases for the Use, Reconstruction and Protection of Animals." The meeting was held on 11-14 February 1975 in the Zoological Institute of the Academy of Sciences of the U.S.S.R. (Leningrad).

These malacological meetings have become a tradition in the U.S.S.R. (the first one took place in November, 1961) and show a continuing strong interest in molluscs and a broadening of the research effort directed toward them. Because of this widening interest, the themes dealt with at the Fifth Meeting varied greatly. Side by side with works on taxonomy, fauna history and ecology of molluscs, papers were presented on new methods of investigation (such as kariotaxonomy, caryology, cytotaxonomy, protein electrophoresis, etc.). Some aspects of cephalopods were considered for the first time. A number of papers dealt with the part molluscs play in the precise identification of borders between Mesozoic and Cenozoic times (a very important problem, from both theoretical and practical viewpoints).

All inquiries concerning these Meetings should be addressed to the Malacological Committee, Zoological Institute, the U.S.S.R. Academy of Sciences, Universitetskaya naberezhnaya 1, Leningrad, B-164, U.S.S.R.

ABSTRACTS

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NEW DATA FOR CONSTRUCTING A SYSTEM OF CLASSIFICATION FOR THE BIVALVIA

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Abstract

Since the publication of the paper by Nevesskaya, Scarlato, Starobogatov & Eberzin (1971) dealing with the systematics of the Bivalvia, new materials have been accumulated which can be used for the elaboration of their classification. A study of the anatomy of antarctic *"Silicula" rouchi* Lamy conducted by Egorova and Starobogatov suggests the erection of the new suborder Radiidentina in the order Ctenodontida (the genus *Radiidens* Egorova & Starobogatov is a new name for *Silicula* Thiele 1935, *non* Jeffreys 1879 [type species *S. fragilis* Jeffreys 1879]; the name *Silicula* was introduced by Jeffreys as a substitution for *Phaseolus*). The new suborder is characterized by phaseloid dentition, a strongly enlarged hepatic duct opening in the left pouch, a well-developed cuticular lining which spreads to the larger portion of the inner stomach surface, and a poorly developed muscular ridge, which is a continuation of the minor typhlosole. The suborder includes the superfamilies Phaseoloidea and Radiidentoidea (the latter with the single family Radiidentidae Egorova & Starobogatov, in which the posterior portion of the shell is longer than the anterior one, and a resilium and mantle sinus are present). The other families of the order, which have nuculoid dentition, a gastric shield and a well-developed ridge continuing as the minor typhosole, are naturally grouped into the suborder Ctenodontina Douville 1912. It should be noted that the Radiidentina occupy a primitive position, and lead us to a conclusion about the peculiarities of other groups. The formation of the gastric shield and the perpendicular parts of the teeth, with a further polymerization of the latter, are the diagnostic characters of the Ctenodontina. Hypertrophy of the cuticular lining and partial or complete reduction of the radial parts of the teeth, or reduction of the teeth as a whole, are the diagnostic characters of the Solemyida. The displacement of the process of teeth formation to earlier stages (which results in the fixing of their number) presents the lyrodesmoid dentition of the Actinodontida.

A possibility of a direct phylogenetic connection between the Radiidentina and the Solemyida excludes the Praecardiida from the Protobranchia. In addition, in the Protobranchia, the umbones are medial or displaced posteriorly (the apparent displacement anteriorly is caused by the growing of the hind portion of the shell), while in the Autobranchia and the Septibranchia the umbones are shifted or bent forward. This can be easily associated with the fact that the Protobranchia obtain food by labial palps, while members of the 2 other groups obtain food by means of mantle formations of the hind end of the body. In this connection, the noticeably bent or even anteriorly shifted umbones of the Praecardiida indicate that this order does not belong to the Protobranchia. Thus, the Praecardiida are undoubtedly Autobranchia; apparently they are a collective group consisting of representatives of the Cyrtodontida and the Pholadomyida. However, because of insufficient study, the Praecardiida should be regarded as a distinct order and placed somewhere close to the Pholadomyida.

The status of the suborder Ostreina is questionable because its characters (except the ratio between the parts of the major typhlosole) are associated with the development of its oyster-like form ("ostreization") and which, to the same extent, is typical of the oyster-like Actinodontida (deliberately polyphyletic). The group Ostreina is obviously diphyletic (Stenzel, 1971). This is shown, first of all, not by the characters mentioned by Stenzel as they can reflect different stages of ostreization, but by sharp differences in the structure of the provincula, which is not connected with ostreization. The structure of the stomach, and the possibility of the comparison of chomata with the secondary multidentate dentition of Mytilidae, closely relate oysters to the Arcina. This is also indicated by the presence of Quenstedt's muscle, a homologue of the protractor, and this, in turn, indicates that oysters originated from dimyarian ancestors. This suggests that oysters are 2 distinct superfamilies of the suborder Arcina, Gryphaeoidea and Ostreoidea. As to the families Chondrodontidae and Lithoiotidae, they should be conditionally included in the order Pectinida (Freneix & Lefevre, 1967; Reis, 1903), or the later family, the Lithoiotidae, perhaps in the order Hippuritida. The superfamily Cyrtodontoidea, to the contrary, deserves the distinct status

of suborder (Cyrtodontina Scarlato & Starobogatov 1971), representatives of which are characterized by cyrtodont dentition (there is also a group with radially diverging subumbonal teeth; Pojeta, 1971).

This dentition is closer to the primitive forms of pterineoid dentition, but in the latter the submarginal (hind) teeth are developed along the whole length and not limited by hind portions as in the cyrodont type. Due to the diversity of the members of the Astartida, the order can be divided into 4 suborders. The suborder Astartina Scarlato & Starobogatov 1971 includes forms with the astartoid dentition or, to a certain extent, with a simplified or reduced dentition, a well-developed left pouch of the stomach and united lumens of the midgut and style sac (superfamilies Astartoidea, Crassatelloidea, Hiatelloidea, Cyrenoidoidea, Pisidioidea and Mactromyoidea - in the ranges of the families Mactromyidae and Fimbriidae). The suborder Lucinina Stoliczka 1870 includes forms with the lucinoid dentition, reduced left pouch of the stomach and united lumens of the midgut and style sac (corresponds to the superfamily Lucinoidea without the Mactromyidae and the Fimbriidae). The suborder Leptonina Scarlato & Starobogatov 1975 includes forms with the lucinoid or "paracyrenoid" dentition (Chavan, 1953), with a developed left pouch of the stomach and isolated lumens of the midgut and style sac (superfamilies Donacoidea, Cyamoidea, Kellioidea, Leptonoidea and Galeommatoidea). The suborder Chlamydoconchina Scarlato & Starobogatov 1975 includes forms lacking adductor muscles and hinge, and having an inner rudimentary shell (corresponds to the superfamily Chlamydoconchoidea).

In the limits of the gigantic order Venerida, the suborder Venerina which includes most of the families, is divided, due to its heterogeneity, into 3 distinct suborders. The suborder Cardiina Fischer 1887 includes forms with lucinoid dentition (tooth 2 is represented only by the whole or bifurcate 2b), a spirally twisted free end of the major typhlosole (sometimes the spiral is reduced to a loop), and relatively approximated gastric caeca and united lumens of the midgut and style sac (superfamilies Cardioidea, Tridacnoidea, Ungulinoidea, Tellinoidea and Scrobicularioidea). The suborder Veneriña includes forms with the arctoid (cyprinoid) or corbiculoid (= cyrenoid) dentition, which is sometimes partially or completely reduced, the major typhlosole, without a spirally twisted free end, greatly approximated gastric caeca (they are twice as close to each other than to the entrance to the midgut), and with united lumens of the midgut and style sac (superfamilies Arcticoidea, Kellielloidea, Gaimardioidea, Glossoidea, Corbiculoidea, Veneroidea and Pleurodesmatoidea). The suborder Myina Stoliczka 1870 includes those forms with dentition which resembles the lucinoid type, often partially or completely reduced, but which was formed independently of the arcicoid dentition (tooth 2 is represented both by the whole 2b and the newly formed 2a, but tooth 1 is not isolated; such a hinge can be called mactroid). The major typhlosole is not twisted into a spiral free end, and the lumens of the midgut and the style sac are well separated (superfamilies Mactroidea, Solenoidea, Myoidea and Dreissenoidea).

Conocardiids, which were assigned by Nevesskaya et al. (1971) to the order Cuspidariida, recently (with addition of the genera *Eopteria* and *Euchasma*) have been separated (Pojeta, Runnegar, Morris & Newell, 1972) into a distinct class Rostroconchia by the consideration that its members possess an entirely tubular protoconch. This argument is, however, not very convincing in as much as such a protoconch cannot be rigidly connected with both valves of the bivalve shell (this runs counter to the evolutionary tasks asking for the formation of 2 mobile valves). The rostral end of the shell in conocardiids should be considered an anterior one, which proceeds from the position of the ventral (byssal) notch between the valves in *Conocardium* and from the mantle sinus in *Eopteria*. What was taken for the protoconch can be easily interpreted as a projection of the ligament (opisthodetic). The lower row of small muscular imprints in *Eopteria* is interpreted as imprints of septal muscles (there are homologues in *Conocardium*). Besides, the direct flow of water (from the counterrostral to the rostral end) is sufficient for the septal water-motive mechanism and has no advantages for the ciliary mechanism. Therefore, conocardiids should be retained in the range of the Septibranchia and separated into a distinct order, the Conocardiida Neumayr 1891. Their sessile mode of life (filtering rather than predatory feeding), direct waterflow and, undoubtedly, specificity of structure and function of the septum, speak in favor of this. Most of the genera of the Lunulicardiidae (excluding *Lunulicardium* and *Pterochenia*) and Ribeiriidae (excluding *Ribeiria*) should be referred to the order Conocardiida. Ribeiriidae (excluding the type genus of the family) are undoubtedly bivalve mollusks (according to the structure and growth of the shell). A number of Lunulicardiidae are associated with *Conocardium* through *Eopteria* and *Euchasma*. The diversity of the genera leads us to group them into several superfamilies: Eopterioidea Miller 1889, Ischyrinioidea Kobayshi 1933 and Conocardioidea Miller 1889.

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ON THE SYSTEMATIC ARRANGEMENT OF EUTHYNEURAN SNAILS

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Abstract

Euthyneuran snails have long been grouped into 2 subclasses, the Opisthobranchia and the Pulmonata. During the past decades they have been united into the subclass Euthyneura, opposite the Streptoneura (= Prosobranchia). In both cases, they are considered to be higher mollusks and to have been derived from the Prosobranchia. However, the presence in most Euthyneura of a wide multidentate ("musivoglossate") radula which is more primitive than all known radulae of Prosobranchia ("arthroglossate") contradicts this.

In regard to the structure of the mantle complex, Euthyneura are very diverse. Whereas in most Opisthobranchia (and in most Prosobranchia as well) the left half of the mantle complex is retained, it has been shown (Pötsch, 1904; Ghose, 1963) that in the Pulmonata the remaining kidney is the one of the right, and so the auricle (where the blood from the right kidney enters) must be the right one also. Besides, according to the innervation (Stiglingh, van Eeden & Ryke, 1962; Walter, 1969), the pseudobranch in the Pulmonata, and in its absence, a part of the anal lobe, is homologous to the right ctenidium. All this indicates that in the Pulmonata the right rather than the left half of the mantle complex has been retained. It should be stressed that during all evolutionary reconstructions of the mantle complex, the kidney (more precisely the nephropore) and gill retain their primary interlocation. If the left half of the complex is reduced, the base of the ctenidium lies to the right side from the nephropore; if the right half is reduced, then the base of the ctenidium lies to the left. This suggests that in some groups assigned to the Opisthobranchia, the left half of the mantle complex is also reduced. For example, the same correlation as in the Pulmonata can be found in those members of the Thecosomata (*Peracle*), Umbraculidae, Tylodinidae and Runcinidae that preserve the gill. This leads us to oppose the above groups (together with the anatomically close abranchiate Thecosomata and Acochlidiidae) to the other Opisthobranchia. A study of the innervation of the internal organs in the Pulmonata led Hubendick (1947) to the conclusion that the zygosis hypothesis for the origin of euthyneuria as advanced by Krull (1935) holds for this group too. This is also borne out by the retention of the right half of the mantle complex in this group. Reverse relations in "typical" Opisthobranchia (including those which did not undergo detorsion) speak in favor of the application to them of the connective hypothesis advanced for Euthyneura by Naef (1911) and Merker (1913). As to "aberrant" Opisthobranchia, the origin of euthyneuria in them is assumed to be the same as in the Pulmonata due to the retention of the right half of the mantle complex.

In the Siphonariidae, which are usually assigned to the Pulmonata, a part of the gill (with its branchial vein) lies to the left of the nephropore, whereas the other part (also with a special vein) lies to the right. In addition to 2 branchial veins, 2 separate renal veins open into the auricle. This suggests that the mantle complex of this group was formed by means of the fusion of the initially paired complex, which separates them from the other Euthyneura.

Both lower Opisthobranchia and lower Pulmonata demonstrate distinct heterostrophy. Later on, heterostrophy disappears, but there remains a trace of heteraxiality – a columellar fold (Meyer, 1955). However, this fold sometimes acquires a special function. To the contrary, in "aberrant" Opisthobranchia (Thecosomata, Umbraculidae, Tylodinidae, Runcinidae and Acochlidiidae) heterostrophy has never been observed. The shell either preserves its initial hyperstrophic state (Minichev & Starobogatov, 1971a), as in spiral Thecosomata and Umbraculidae-Tylodinidae (only traces of hyperstrophy), becomes bilaterally symmetrical (non-spiral Thecosomata, Runcinidae), or is discarded (Acochlidiidae, higher Pseudothecosomata). It is precisely discarded, rather than reduced under the mantle as in the other gastropods. In the Siphonariidae, there is neither heterostrophy nor hyperstrophy. Their embryonic shell is planispiral and variations permitting it to be regarded either as sinistral or dextral arise due to differences in overlapping of 2 successive whorls (Hubendick, 1947).

Thus, in the ranges of Euthyneura, 4 groups are arranged: 1, Siphonariidae; 2, Pulmonata; 3, "typical" Opisthobranchia; and 4, "aberrant" Opisthobranchia. A very important character of the latter, in addition to the ones mentioned, is the tendency to complete detorsion. In this case, in aberrant groups, the turn is realized, in general, not by means of differential growth but by means of rapid displacement of the whole mantle complex (Thecosomata). This displacement proceeds not along the longitudinal axis of the visceral sac (with the simultaneous fusion of the latter with the cephalo-pedal mass as in typical Opisthobranchia), but around its base (Thecosomata, Acochlidiidae and Umbraculidae). In this respect, Opisthopneumona do not differ from aberrant Opisthobranchia. Moreover, in the structure of the mantle cavity of these groups, a significant resemblance is recognized: their initial forms have a very narrow

tube-shaped cavity (Euthecosomata, Acochlidiidae and Onchidiidae) which in higher representatives (Pseudothecosomata, Runcinidae, Rhodopidae, etc.) is reduced.

All of these data point to an independent origin from ancient Diotocardia of the 4 above groups. They are distinct and equivalent phylogenetic stems which should be considered subclasses: 1, Divasibranchia (= Siphonariidae); 2, Pulmonata; 3, Opisthobranchia; and 4, Dextrobranchia (= "aberrant" Opisthobranchia + Opisthopneumona).

Some words about the orders composing each subclass follow. The subclass Divasibranchia consists of the single order Siphonariida. Within the ranges of the Pulmonata, the Basommatophora and the Stylommatophora undoubtedly represent natural groups. Their status, however, should be raised to a superorder, since each of them is so heterogenous that it should be divided into several orders. According to Minichev & Slavoshevskaya (1971), the Stylommatophora should be divided into the orders Helicida (= Geophila), Succineida, Ailyida and Athoracophorida (= Tracheopulmonata). Analogously, the Basommatophora is separated (Starobogatov, 1970) into the Amphibolida, Ellobiida (= Actophila), Limnaeida (= Hygrophila) and Trimusculida (the latter includes only Trimusculidae with diaulic reproductive systems and cephalic shields).

In the ranges of the Opisthobranchia, most of the orders (Aplysiida = Anaspidea, Philinoglossida, Pneumodermatida=Gymnosomata, Cylindrobullida, Acteonida, Doridida=Anthobranchia and Aeolidiida=Nudibranchia) are quite distinct and their sizes are about equal. The other members of the Notaspidea form the order Pleurobranchida. The Cephalaspidea includes 2 orders: the Bullida, which consists of the forms with monaulic reproductive systems, and the Diaphanida, which have oodiaulic reproductive systems. The Sacoglossa, despite the fact that it represents quite a natural group, should be divided into 3 orders due to the diversity of its members: Oxynoida (having a spiral shell), Elysiida (triaulic forms without a shell), and Juliida (forms with bivalve shells). The orders are grouped into 3 superorders: the Tectibranchia (orders Bullida, Philinoglossida, Diaphanida, Aplysiida and Pneumodermatida), Acteobranchia (orders Acteonida, Pleurobranchida, Doridida and Aeolidiida) and Sacoglossa (orders Cylindrobullida, Oxynoida, Elysiida and Juliida). It is possible that some families of the superorder Pyramidellimorpha (Golikov & Starobogatov, 1975), the Pyramidellidae, Architectonicidae and Mathildidae in particular, and also some other families, should be placed into the same subclass and form a distinct superorder with several orders. At the same time, the Subulitidae and Vellainellidae, assigned to the same superorder, are undoubtedly Ellobiida (Pulmonata); Loxonematoidea is closer to Murchisonioidea (Scutibranchia).

The orders assigned to the Dextrobranchia are also distinct, and only the Thecosomata should be divided into 2 orders: Peraclida (= Pseudothecosomata), having a single fin and a proboscis, and Cavoliniida (Euthecosomata) with paired fins and without a proboscis.

The orders of this subclass are grouped into 4 superorders: the Thecosomata (orders Peraclida and Cavoliniida), Acochlidia (order Acochlidiida), Notaspidea (orders Umbraculida and Runcinida) and Systellommatophora (= Soleolifera, Opisthopneumona) (orders Onchidiida, Rhodopida, Veronicellida).

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PECULIARITIES OF THE STRUCTURE OF THE EXCRETORY SYSTEM OF THE PULMONATA IN RELATION TO SUBCLASS CLASSIFICATION

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Abstract

The excretory system of the Pulmonata is represented by one nephridium ("kidney"), and in many cases it is complicated by excretory ducts – the primary and secondary ureters.

In the Basommatophora, the kidney is more or less uniform, except in those forms with a limpet-shaped shell and a reduced mantle cavity. In the Stylommatophora, the nephridial apparatus is the basis for dividing the order into 4 suborders. In Stylommatophora the condition, which is observed in members of the suborder Mesurethra, is sometimes considered a primary condition. Here the kidney, without ureters, borders the pericardium on the right (on the left in sinistral forms) and the opening of the kidney is displaced somewhat to the left side and never apically. More often, however, the Mesurethra are considered to be a derivative of the Orthurethra, in which the nephridial duct goes away apically from the kidney and usually is called a primary ureter.

The Sigmurethra are characterized by the following peculiarities: the primary ureter, going away from the kidney near its end, goes along the lateral surface of the kidney, then forms a curve abruptly in the depth of the mantle cavity and continues as the secondary ureter, which runs beside the rectum and opens near the anus.

Members of the Heterurethra are characterized by the transverse position of the kidney. The primary ureter, beginning near the pericardium, passes along the frontal surface of the nephridium and then along the rectum. It is essential in this case for the kidney to be somewhat submerged into the visceral mass.

Investigations of vast material have shown that the kidney, as well as both sections of the ureter, are indispensable accessories of the excretory system in all Stylommatophora, although the ureters are sometimes poorly developed. Even in the Orthurethra, the ureters are present as open ciliary grooves (Schileyko, 1976). Consequently, sigmurethria in the evident or vague form is characteristic of all Stylommatophora, and premises as to its origin can be observed in the Ellobiidae. These premises are expressed in the corresponding distribution of the ciliary elements in the mantle cavity. True sigmurethria, where the kidney is shortened and the ureters are distinct, clearly isolated and completely or partially closed, takes place only in the higher Stylommatophora.

The adequacy of phylogenetic speculations depends on the true estimation of the orthurethral type, inasmuch as the kidney in primitive aquatic pulmonates is of that type. In such Orthurethra as, for example, the Enidae, the kidney, in its main features, resembles that of primitive pulmonates. The width of the kidney decreases gradually from the pericardium to the mantle collar, i. e., the outwardly distal part of the kidney does not differ from the proximal one, and morphologically the kidney is an indivisible organ. The excretory apparatus of other Orthurethra has one difference: the distal part of the kidney is narrowed sharply. This narrow part is interpreted as a primary ureter; accepting such an interpretation we cannot but agree that the narrow part was bent at its base during phylogenetic development, transforming the excretory system of the orthurethrous type into the sigmurethrous type. But, the narrow part of the kidney, together with the pulmonary vein, forms topographically an associated system evolving as a whole. Hence, if the narrow part of the kidney is homologous with the primary ureter of the Sigmurethra, then the pulmonary vein must also curve and accompany the primary ureter; but, as a matter of fact, such a pattern is absent.

Thus, orthurethria, at least in the obvious form, is an initial condition for the excretory system of the Stylommatophora. In such a group as the Enidae, there are no essential changes in comparison to hypothetic ancestral forms. Further development of the system consists in a differentiation of the nephridium into a voluminous proximal part and the narrow distal one, the main excretory function being fulfilled by the proximal part, and the distal part tends to shorten. Independently, the nephridial ducts, the primary and secondary ureters, become isolated morphologically. The extreme degree of shortening of the distal part of the kidney, with a retention of open nephridial ducts, results in the formation of mesurethria; the closing of these ducts results in the formation of sigmurethria.

An evaluation of the nephridium of the heterurethrous type has caused numerous discussions, because heterurethria is characteristic of peculiar groups such as the Succineidae, Ailyidae and Athoracophoridae. As a matter of fact, heterurethria is not a rare phenomenon and it appears, as a rule, in all groups where a reduction of the mantle cavity occurs – in some Endodontidae, Helicarionidae, Urocyclidae, Vitrinidae, etc. With the shortening and widening of the lung cavity, the first stages of its reduction proceed the submerging of the kidney into the visceral sac (this phenomenon is connected with an increasing necessity for maximum release of respiratory surface) and an increasing of the angle between the pulmonary vein and the middle lung line. Under such circumstances, the kidney changes, either morphologically (i. e., by becoming shorter, e. g., in some Endodontidae) or topographically (i. e., is rotated, e. g., in some Vitrinidae, Succineidae and Helicarionidae; the rotation may be either clockwise or counter-clockwise). The heterurethrous type, then, may arise as a derivative of the sigmurethrous condition, and probably directly from a little-differentiated kidney of the lower Pulmonata, inasmuch as there are no reasons to consider that the Succineidae arose from some group of higher Stylommatophora.

This testifies that the morphological state of the renopericardial apparatus may not be used as a principle criterion for the elaboration of the systematics and phylogeny in the Pulmonata in general, since the evolution of this apparatus in all taxa proceeded in one direction – deliverance, as far as it is possible, of the mantle cavity ceiling from the excretory organs. In the land mollusks there is a clear tendency – displacement of the kidney and primary ureter to the depth of the pallial cavity for the increase of a respiratory surface. This displacement is expressed in its clearest form in the higher Stylommatophora with many-whorled shells, i. e., those with a long lung. However, with whorls increasing more rapidly in size in some snails, further changes take place which lead to the transformation of sigmurethria into heterurethria.

The orthurethral type, as was stated above, is an initial condition, and therefore the Orthurethra as a taxonomic unit is a valid one. However, the existence of such a unit suggests the existence of other units of the same rank. The promotion of the Sigmurethra as a similar unit has no grounds, since there are no reasons to expect that the Sigmurethra are monophyletic. On the contrary, sigmurethria is a most perfect

condition of the excretory system, and the evolution of any group of land Pulmonata inevitably leads to this condition. Heterurethria in one or another form is a natural result of changes in the sigmurethrous kidney, and accompanies a rather considerable lung reduction.

On the whole, I think that the promotion of the above groups as main units (suborders) of the Stylommatophora is not worthwhile. On the other hand, peculiarities of the structure of the excretory system present suitable material for reconstructing phylogenetic relationships within narrower taxonomic units – within families and superfamilies. In the limits of the Stylommatophora, there are some taxa which clearly can be given superfamily status. Determining the boundaries, size, number and phylogenetic connections between these superfamilies more precisely will serve as a basis for systematic elaboration within the Stylommatophora.

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THE ORIGIN OF THE NERVOUS SYSTEM IN THE MOLLUSCA

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Abstract

The problem of the formation of the nervous system in mollusks is closely associated with the origin of the phylum. If the hypothesis of a turbellarian origin is assumed, then the nervous system of mollusks arises from the orthagon of lower worms. The recognition of an annelid affinity requires a comparison of the abdominal nervous chain of annelids with the longitudinal cords of mollusks. The turbellarian hypothesis advanced by Salvini-Plawen (1972) postulates amerity of mollusks, the absence or independent appearance of the coelom and the presence of an oligomerous orthagon. However, mollusks can be called amere only because they possess a nonsegmented coelom, the formation of which results from their "larval" nature. The development of large paired cavities from primary mesoblasts in the larvae of chitons is good evidence of the annelid origin of mollusks. Besides, there are great pro-morphological differences between Turbellaria and Mollusca: the former are protaxonic, the latter are plagyaxonic. The peculiarities of the development and organization of the Polyclada suggest that this group originated independently from other Turbellaria. Plagyaxony in its representatives is not comparable to that of trochophorate animals, including mollusks.

The nervous systems of mollusks and annelids appear during phylogenesis due to the differentiation of the circumblastoporal plexus in their ancestors (Beklemishev, 1944). Annelids lack the orthogonal nervous system; their nervous net (orthogonoid; see Minichev & Bubko, 1973) is formed as a result of unification of the abdominal cords and segmentary nerves with secondary (peripheral) nerves. Accepting the close relationship between mollusks and annelids, we must then establish the homology of the main parts of the nervous apparatus. Cerebral centers are homologous in both groups. They are formed during ontogenesis in a similar way from the same anlagen. Pedal cords in mollusks correspond to abdominal (connective) cords in annelids. In both cases, they are formed from independent ectodermal anlagen, which later come into contact with cerebral centers. In addition, they have similar main zones of innervation, thus providing for movement of these animals. In annelids, no structures analogous to the pleuro-visceral cords of mollusks have been discovered. Two hypotheses can be suggested to explain the formation of these cords: (1) during phylogenesis pleuro-visceral connectives are formed secondarily from the neural plexus in connection with the development of typical molluscan peculiarities, especially the mantle complex; (2) the pleuro-visceral cords are derivatives of the primary pedal cords. If the first hypothesis is assumed, then it should be expected that both pairs of cords are formed at different times. Indeed, in *Neomenia carinata* (Aplacophora), pleuro-visceral cords are formed later and in a different way; they represent caudal projections of the cerebral part (Thompson, 1960). Larvae of *Tonicella* sp. (Polyplacophora), in which the shell gland is not yet divided into separate portions, also have only one pair of longitudinal (pedal) cords; the pleuro-visceral cords are formed simultaneously with the formation of the shell plates. Such a type of development of the nervous system should be regarded as a primary one. In some Amphineura both pairs of cords are formed at the same time.

Assuming that the pleuro-visceral cords are derivatives of the pedal cords, then forms with only one pair of cords can be expected; but such forms are not yet known. However, in some Chaetodermatidae, different connectives form a common cord in the hind portion of the body, which passes along the wall of the mantle cavity. A similar picture is observed in the anterior end – both connectives of each side be-

gin with the undivided cord; the cord length is different in different species. It should be noted that in young individuals, indivisible portions are relatively longer – their length can exceed 1/2 of the whole length of the mollusk's body. Proceeding from this, we may think of the initial type of nervous system of the Aplacophora (and of all mollusks as well) as being a single non-differentiated ring which later begins to separate into 2 pairs of cords in lateral portions. A possibility of such a morphological separation is proved by rather peculiar relationships in some polychaetes, including *Lisippe labiata* and *Anobothrus gracilis* – each abdominal cord is divided (especially in the hind portion of the body) into 2 isolated cords with small segmental gangliose thickenings. As a result, a nervous system is formed which corresponds to that of lower mollusks. In both cases, there are 2 pairs of longitudinal cords united by transverse commissures with metameric nerves branching to the walls of the body.

Apparently both hypotheses are true and only together can explain the origin of the nervous system of mollusks. The nervous system was formed in parallel with the development of the main peculiarities of the type as a result of differentiation of the ancestral circumblastoporal nervous ring which occurred at different times. The 2nd stage of differentiation proceeded at the period when the ring had a plastic, morphologically unstable character.

Potential abilities of the nervous system for reconstruction are rather high, which is proved by a repeated formation of the orthogonoid type in annelids and arthropods, and the secondary nervous centers (rhinophoral, genital) in gastropods, etc. Of great interest are the mantle nerves on the Docoglossa; they can be compared to the symmetrical mantle nerves of the Zygobranchia, since they show similar areas of innervation and sites of branching. But members of the 1st group have a ring (as the pleuro-visceral arch in the Amphineura), are connected by metameric commissures with pedal cords, contain numerous ganglionic cells and represent a part of the central portion (rather than a peripheral one in the Zygobranchia) of the nervous system. Apparently the mantle cords of the Docoglossa, as well as the pleuro-visceral ones, are derivatives of the primary circumblastoporal ring.

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SOME PROBLEMS IN THE CLASSIFICATION OF THE ORDER DENTALIIDA (MOLLUSCA; SCAPHOPODA)

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Abstract

A careful study of radular structure and soft body morphology of 24 species belonging to 11 genera of the order Dentaliida has brought to light the fact that the accepted classification of the order is based on conchological characters which are to a considerable extent unsound and artificial. The genera examined were found to differ markedly in the structure of their radulae.

The most common type of radula, the "Antalis type", is notable for the wavy contour of the marginal teeth, which have 2 curvatures, and for lateral teeth having an abruptly sharpened projection pointed forward where the tooth is bent in such a manner that nearly a right angle is formed. Animals with this type of radula can be arranged into 3 groups according to the shape of central teeth: (1) those with "simple" teeth (*Antalis, Paradentalium, Striodentalium, Calliodentalium*); (2) those with teeth having a transversal ridge (*Fissidentalium*); and (3) those with teeth that are longitudinally broadly thickened while the lateral and posterior margins remain thin (*Episiphon* and *Anulidentalium*).

Radulae of the "Rhabdus type" differ sharply from those of the preceding type, occasionally to such an extent that definite dental parts and structures cannot be homologized with any of those of the "Antalis type". *Rhabdus, Eboreidens* and *Omniglypta* have such radulae.

In *Antalis, Paradentalium, Fissidentalium* and *Striodentalium*, the epipodial collar of the foot is almost wholly interrupted on the ventral side (the incision almost reaches the body of the foot and, consequently, separate lobes are formed). In other genera, these lobes knit together ventrally (partly in *Pseudantalis, Episiphon* and *Calliodentalium*, or wholly in *Rhabdus* and *Eboreidens*).

Within the genera studied, types prevail in which the inner pair of retractors is wider than the exterior ones. This difference between the pairs of the named muscles is slight in *Antalis, Paradentalium, Striodentalium* and *Fissidentalium*; it is markedly manifested in *Pseudantalis* and *Calliodentalium*, and is quite distinct in *Episiphon* and *Anulidentalium*. In *Rhabdus* and *Eboreidens*, these pairs of muscles have the same width.

The above mentioned 4 groups of genera differ from each other by a distinctive form and structure of the mantle valve[1]. In the 1st group it is represented by a rounded opening with gathered margins; in the 2nd group the valve has a form of transversal slit; in the 3rd group the valve is as in the 2nd, but there is a circular fringing fold on the anterior surface of the mantle which is interrupted at the ends of the slit. In the 4th group the valve is U-shaped and the upper half of the fringing fold is bent towards the upper flap of the valve.

According to the peculiar characters of the radula and shell structure, 2 new genera have been established by the author.

Eboreidens Chistikov 1975 (Type species: *Dentalium lacteum* Deshayes, 1825). Shell of medium size, narrow, thin, slightly curved, polished, translucent and with low irregular transversal swellings. Aperture and apical orifice circular, the latter sometimes slightly notched on its ventral margin. Soft parts as in *Rhabdus*. Central teeth of the radula triangular, each with 2 rhomboidal cusps. Lateral teeth subcylindrical, their "heads"[2] not differentiated from their "handles"; supporting surface separated from the upper surface by a sharp rib. No dental crests; no postmedial cusps; medial cusps pyramidal, with a denticulated descending margin. Marginal teeth slightly arched.

Anulidentalium Chistikov 1975 (Type species: *A. bambusa* Chistikov). Shell stout, needle-shaped, smooth, polished, laterally compressed, regularly annulated with rings which break up its exterior surface into long segments as in bamboo. Inner surface of the middle part of the shell with a groove on its ventral side. Foot with a ventral ridge; epipodial collar not oblique. Other parts of the body as in *Episiphon*. Central teeth with thin plates, situated at 2 anterior angles and with 3 longitudinal ridges. Postmedial cusps of lateral teeth pushed far backwards toward the lower margin of the posterior surface.

Anulidentalium bambusa Chistikov 1975. Shell almost straight, semitransparent, ovoid in cross section (its dorso-lateral surfaces flattened). Aperture nearly straight, with thin margins. Apical orifice circular, slightly notched on its ventral side. Longitudinal ridges of the central teeth protrude forward as cusps. Lateral teeth each with 3 medial and 2 postmedial cusps; the posterior margin of their inner surface bears a cusp. Shell length 40 mm. Dorsoventral diameter of the aperture 1.25 mm; lateral diameter 1.10 mm. Diameter near the apex 0.2 mm. Height of the curvature 0.9 mm. This species is common in the Gulf of Tonkin, where it occurs at a depth of 38 to 75 m.

A synthesis of conchological characters of the known genera with my data permits a new classification of the order Dentaliida as follows.

Order Dentaliida[3] Da Costa 1776.

A. Superfamily Quasidentalioidea Chistikov 1975. Includes a single family.
   I. Family Quasidentaliidae Chistikov 1975. Shell massive, with numerous longitudinal ribs and a single muscle impression (the foot probably had a creeping sole). Represented only by the type genus – *Quasidentalium* Shimansky 1974.

B. Superfamily Dentalioidea Gray 1834. Includes 4 families.
   I. Family Prodentaliidae Starobogatov 1974. Represented only by the type genus – *Prodentalium* Young 1942.
   II. Family Dentaliidae Gray 1834. Includes 3 subfamilies.
      1. Subfamily Dentaliidae Gray 1834. Represented by *Dentalium* Linnaeus 1758, *Coccodentalium* Sacco 1896, *Fissidentalium* Fischer 1885, *Compressidentalium* Habe 1963 and *Schizodentalium* Sowerby 1894.
      2. Subfamily Antalinae Stoliczka 1858. Differs from the preceding subfamily by the small number of medial cusps on the lateral teeth and by the distinct proportions of marginal teeth. Represented by *Antalis* H. & A. Adams 1854, *Lentigodentalium* Habe 1963, *Paradentalium* Cotton & Godfrey 1933, *Striodentalium* Habe 1964, *Heteroschismoides* Ludbrook 1960, *Spadentalina* Habe 1963, *Tesseracme*[4] Pilsbry & Sharp 1898, *Graptacme*[4] Pilsbry & Sharp 1897 and *Fustiaria*[4] Stoliczka 1868.

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[1] The mantle valve signifies here the assemblage of structures of the anterior portion of the mantle responsible for closing the entrance into the mantle cavity.

[2] The distal "workable" portion of the tooth, usually delimited by a constriction from the rest of the tooth ("the handle"), is named here the "head".

[3] The succession in taxa in this list reflects their supposed affinity and increasing specialization. I believe that the Plagioglyptidae Starobogatov 1974 should be considered as a separate order.

[4] Taxonomic status and/or position of the taxon need further examination and discussion.

3. Subfamily Calliodentaliinae Chistikov 1975. Shell with no sculpture, inner pair of retractors markedly wider than exterior pair, foot with a ventrally notched collar, mantle valve with 2 flaps. Radula as in Antalinae. Represented by *Laevidentalium*[4] Cossman 1888, *Calliodentalium* Habe 1964 and *Pseudantalis* Monterosato 1884.

III. Family Gadilinidae[4] Chistikov 1975. Shell with 1-4 sharp keels. Represented by *Gadilina* Foresti 1895 and *Bathoxiphus*[4] Pilsbry & Sharp 1897.

IV. Family Episiphonidae Chistikov 1975. Shell with or without annular sculpture, needle-shaped. Inner and exterior pairs of retractors differ sharply in width. Foot with a ventrally notched collar. Mantle valve with 2 flaps and a fringing fold. The proportions of the marginal teeth are characteristic. Includes 3 subfamilies.

1. Subfamily Episiphoninae Chistikov 1975. Shell smooth. Apex with a tube. Central teeth thickened. Upper cusp of the lateral teeth large and pushed far backwards toward the "handle". Represented by a single genus – *Episiphon* Pilsbry & Sharp 1897.
2. Subfamily Anulidentaliinae Chistikov 1975. Shell with annular sculpture, inside with a shallow groove on its ventral side. Central teeth of radula each with 3 longitudinal ridges. Represented only by the type genus – *Anulidentalium* Chistikov 1975.
3. Subfamily Lobantalinae Chistikov 1975. Shell smooth, inside with 2 lateral ribs. Represented by a single genus – *Lobantale* Cossmann 1888.

C. Superfamily Rhabdoidea Chistikov 1975. Includes 3 families.

I. Family Rhabdidae Chistikov 1975. Shell with no regular sculpture, nearly straight. Inner and outer pairs of retractors of the same width. Pedal collar without a notch. Mantle valve U-shaped, with a fringing fold. Central teeth trapezoidal in shape. Lateral teeth with numerous obscure dental crests, postmedial cusps very large. Represented by a single genus – *Rhabdus* Pilsbry & Sharp 1897.

II. Family Eboreidentidae Chistikov 1975. Shell with no regular sculpture, slightly curved. Soft body as in the preceding family. Central teeth triangular, each with 2 rhomboidal cusps. Lateral teeth with no dental crests, and with no postmedial cusps. Represented by a single genus – *Eboreidens* Chistikov 1975.

III. Family Omniglyptidae Chistikov 1975. Shell densely and regularly annulated, nearly straight. Central teeth each with numerous denticles. The proportions of lateral and marginal teeth are characteristic. Represented by a single genus – *Omniglypta* Kuroda & Habe 1953.

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ON THE SYSTEMATICS OF THE POLYPLACOPHORA

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Abstract

At present there are 2 competing (although in some points similar) schemes for classification of the Polyplacophora in the literature. The system suggested by Thiele (1910) is based on the anatomy and conchology of recent representatives of the class, but insufficiently considers fossil forms. The system by Bergenhayn (1930, 1955) lacks this defect, but it is completely conchological, ignoring anatomical peculiarities. In order to make more precise the problems associated with the systematics of the class, it is necessary to analyse the main directions and stages of evolution of some systems of organs.

The shell of the most ancient chitons consisted of 7 plates (II-VIIIa; the plates of recent chitons can be numbered from front to rear; plate VIII, which consists of 2 parts, can be designated as VIIIa+b). This is proved by the presence of these 7 plates in *Septemchiton*, formation of these plates during ontogenesis, and the absence of I and VIIIb in all discoveries of *Chelodes* and *Gotlandochiton*. The second peculiarity is the presence of the same 3 shell layers that occur in all other mollusks. In the most primitive chitons, *Chelodes*, the plates were not divided into areas that reflect non-differentiation of the plate formation zone. In *Septemchiton*, in addition to the anterior zone, lateral zones appear, and thus the plate is divided into 3 areas (1 anterior and 2 lateral). The formation of lateral zones is well detected in more

developed chitons in the morphological series Scanochitonidae-Lepidopleuridae. As far as the perinotum and plates form a closely connected system, the growth of the perinotum leads to an enlargement of the lateral zones. On account of the anterior zone, and instead of the wide anterior (central) and narrow lateral margins, a narrow jugal and wide latero-pleural areas are formed. This process goes on independently in various groups. It is characteristic that the posterior formation zone is always very weak in the intermediate plate; that is why the genus *Llandeilochiton* (it is not yet proved that its shell consisted of several plates) should be unconditionally excluded from the Polyplacophora. The next stage is the appearance of the cephalic plate (I), which serves for the protection of the anterior part, and the creation of a solid support for the buccal musculature (Scanochitonidae). Later (as in ontogenesis), semiplate VIIIb appeared, and, simultaneously with it, very likely the articulamentum of the Lepidopleuridae was formed.

We can consider the inner structure of ancient chitons if we proceed from the assumption that the Aplacophora originated only from the chitons (with the loss of the shell and foot, which are unnecessary for worm-like movement, and the substitution of all other integumentary formations by the perinotum). This point of view can easily be proved by explaining the origin of the median longitudinal fold as only the rudiment of the foot. In this connection, we can conclude that the digestive system of primitive chitons lacked a separated liver and stomach, and had a primitive 1-to-3-rowed radula. Later on, the liver was separated as an unpaired ventral projection (which then became paired), a stomach developed and with the appearance of a solid support for the buccal musculature, the radula became polymerized (the latter is proved by studies of ontogenesis; Minichev & Sirenko, 1974). The initial number of gills and auricles were 1 pair each. The latter single pair of auricles is a result of the fusion of 2 pairs, which is proved by the presence of 2 pairs of atrioventricular openings. Later on (as in many other mollusks leading the same mode of life), the gills become polymerized. Very possibly this proceeded synchronously with the development of semiplate VIIIb. It did not affect the number of auricles, but kidneys (hind coelomoducts) connected functionally with the gills, grew and became more complicated, so that in higher chitons a special pedal duct appeared. The central nervous system of chitons does not undergo considerable changes in evolution. So, we cannot but agree with Bergenhayn's (1955) division of the class into the subclasses Paleoloricata and Neoloricata, limiting the former to only the most ancient forms with 7 segmented shells. In other respects, the systematics of the Paleoloricata remains unchanged. On the other hand, in the range of the Neoloricata, forms with a shell lacking an articulamentum and semiplate VIIIb should be separated into the order Scanochitonida Starobogatov & Sirenko 1975. In addition, in the range of Lepidopleurida (recognized by us as an order), the suborder Choriplacina, which is composed of forms with reduced tegmentum (like Acanthochitonina), should be separated. Apart from the Chloriplacidae, this suborder includes the family Glyptochitonidae, which is characterized by an oval tegmentum on plate VIIIa+b and trapeziform plate I. The other Neoloricata, which form in our opinion the order Chitonida, should be divided into 3, rather than 2, suborders. The suborder Ischnochitonida, erected by Bergenhayn, should be divided into the suborder Tonicellina Starobogatov & Sirenko 1975 (abanally arranged gills; kidneys lacking a pedal duct; a tendency for a fusion of the atrioventricular openings) and the suborder Chitonina (adanally arranged gills; kidneys with a pedal duct; a tendency for polymerization of the atriventricular openings). The similarity of the shells in both suborders can be explained by the preservation of the form characteristic of the initial representatives of the order. It is noteworthy that a greater part of the genera of the old family Ischnochitonidae, together with *Tonicella*, belong to the 1st suborder, and the genus *Ischnochiton* belongs to the 2nd order.

The higher systematics of the class can be presented in the following way: Class Polyplacophora Blainville 1816, Subclass Paleoloricata Bergenhayn 1955, Order Chelodida Bergenhayn 1943, Suborder Chelodina Bergenhayn 1943 (Chelodidae Bergenhayn 1943; Gotlandochitonidae Bergenhayn 1943), Suborder Septemchitonina Bergenhayn 1955 (Septemchitonidae, 1955).

Subclass Neoloricata Bergenhayn 1955, Order Scanochitonida Starobogatov & Sirenko 1975 (Scanochitonidae Bergenhayn 1943); Order Lepidopleurida Thiele 1910, Suborder Lepidopleurina Thiele 1910 (Lepidopleuridae Pilsbry 1892; Hanleyidae Bergenhayn 1955; Afossochitonidae Ashby 1925), Suborder Choriplacina Starobogatov & Sirenko 1975 (Choriplacidae Cotton & Weeding 1939; Glyptochitonidae Starobogatov & Sirenko 1975); Order Chitonida Thiele 1910, Suborder Tonicellina Starobogatov & Sirenko 1975 (Tonicellidae Simroth 1894, Callistoplacidae Pilsbry 1893, Mopaliidae Dall 1889, Chaetopleuridae Rochebrune 1881, Subternochitonidae Bergenhayn 1930, Schizoplacidae Bergenhayn 1955), Suborder Acanthochitonina Bergenhayn 1930 (Acanthochitonidae Pilsbry 1893, Criptoplacidae Dall 1889), Suborder Chitonina Thiele 1910 (Ischnochitonidae Dall 1889, Callochitonidae Plate 1899, Schizochitonidae Dall 1889, Chitonidae Rafinesque 1815).

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ADAPTATIONS OF PELAGIC GASTROPODS

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Abstract

Among pelagic gastropods the best known are the Heteropoda and the "Pteropoda", both of which form large taxonomic subdivisions with numerous species. Other pelagic species belong to groups such as the Janthinidae, Glancidae, Fionidae, etc. An active pelagic mode of life depends, first of all, on the formation of special locomotory organs, which are derivatives of the foot or mantle. Passive movement is associated with the development of special hydrostatic mechanisms reducing the specific gravity of the animals. Especially representative in this respect are some members of the Lamellariidae, particularly the Antarctic *Marseniopsis conica*, in which was found new types of adaptations, developed during embryonal stages and maintained in the definitive forms. Single large eggs of this species are surrounded by a dense mucous coat bearing numerous tubular appendages. These appendages have a complex structure of their walls, and their free ends are provided with a closed, valve-shaped structure which regulates the water entering into the membrane of the clutch. In the developing embryo (at the veliger stage) the following changes take place. The nautiloid shell, bearing high spiral ribs, is surrounded by a large mantle fold. The inner and outer epithelia of this fold gradually diverge from each other, forming an area filled with friably situated solitary connective tissue and muscle elements. Apparently the main component of this cavity is liquid, which serves for the maintenance of the embryo while it is suspended in the water. The tubular appendages are reduced. The embryo membrane retains 2 openings, one on the dorsal side (entering the narrow duct connecting the shell cavity with the environment) and the other, a wider one, on the ventral side entering the mantle cavity. The development of this mollusk can be observed to maturity, which comes when individuals reach 20 mm in diameter. Larger individuals, up to 23 mm in length, also lead a pelagic mode of life (E. N. Gruzov, pers. comm.). Their movement is accomplished by the hydrostatic effect caused by the shell cavity being filled with water. However, it cannot be excluded that the velum, which is preserved in the shape of a many-lobed fold bearing long cilia up to the last developmental stages, also helps in swimming. Cilia create the directed currents of water in the mantle cavity.

Semipassive movement in water (or in the pleuston) can also be accomplished by the accumulation of gas bubbles in the body of the animal. In particular, numerous gas bubbles (probably atmospheric air) in *Glaucilla marginata* fill the large branchings of the liver and the thin branches of the dorsal papillae.

The most characteristic changes which occur during the transition to active swimming take place in the foot. In the Heteropoda, the isolated hind portion of the foot, the metapodium, serves as a swimming organ; in the Thecosomata, lateral folds of the foot, the parapodia, serve this function; while in the Gymnosomata, it is the lateral superpedal folds, the epipodia. A morphological role of the foot in the Heteropoda can be easily detected in the series Atlantidae-Carinariidae-Pterotrachaeidae. The principle difference between the 2 groups of "pteropods" consists in the following: in the Thecosomata (e. g., in *Lamicina helicina*) the fins and foot proper appear as a common formation; the former are the lateral growths of the common anlagen, whereas in the Gymnosomata (e. g., in *Spongiobranchaea australis*) the fins are formed independently (dorso-laterally) from the anlagen of the foot proper. Thus, the analysis of pedal structures (as well as of other organs) confirms the independent origin of 2 groups of "Pteropoda" (Pelseneer, 1888). Moreover, in the Thecosomata, the formation of the swimming organs is accomplished in different ways and in different directions: in the Peraclidae and Cymbulidae the unpaired fin together with the foot is located ventrally from the oral opening, whereas in the Limacinidae and Cavolinidae the paired fins and foot surround the whole oral opening.

The development of lateral pedal folds stipulates, as a rule, a "flapping" character of swimming. However, in higher Anaspidea the pedal folds merge dorsally. A study of *Stylocheilus longicaudatus* and *Notarchus* sp. enabled us to detect a complex muscular system in the walls of the epipodial cavity which provides a "reactive" movement. Observations on *Notarchus indicus* confirm the ability of these mollusks for active swimming by means of pulsating contractions of the cavity.

Active movement by means of derivatives of the mantle, or by bending the whole body, is not very typical of mollusks. *Hexabranchus* (Anthobranchia), in which there are large mantle wings (notopallum), are a prime example of such movement. A peculiarity of the structure of the mantle, as well as the gill and genital apparatus, opposes the Hexabranchidae to most groups of Nudibranchiata.

Analysis of the organization of pelagic gastropods shows that the main adaptive changes take place in the floating or swimming organs; modifications in other systems are correlated with these changes.

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ZOOGEOGRAPHIC CHARACTERISTICS AND ORIGIN OF THE TERRESTRIAL MOLLUSCAN FAUNA OF BULGARIA

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Abstract

Vast collections of land mollusks made by S. G. Damjanov from 1961 to 1970 and by the author during 1967 and 1969 in Bulgaria served as a basis for this report. Two hundred and sixteen species and subspecies of land mollusks have been established for Bulgaria (instead of 153 species as reported by Jaeckel, Klemm & Meise, 1957). Of these, 197 species were used for a zoogeographical analysis (which did not include the 4 species introduced by man and 15 species with an indistinct distribution).

In Bulgaria, as well as in the whole Balkan Peninsula, the following families of land mollusks are most abundant: Clausiliidae, with 30 species; Zonitidae with 27; Hygromiidae with 19; and Helicidae with 18. Most Enidae recorded from the northern Balkan Mountains (16 of 29 species) occur in Bulgaria. Of these, 12 species are reported only from Bulgaria, and European and Asiatic Turkey.

The land malacofauna of Bulgaria comprises 9 zoogeographical groups, as follows.

1. Widely distributed boreal species (trans-holarctic and trans-palaearctic forms) – 23 species. These are cold-resistant and hydrophilous. They inhabit various biotopes in the north, while in the south, including Bulgaria, they are adapted to extrazonal biotopes with high and constant humidity.
2. Common European species – 34 species. In general, these are thermophilous forest mesophils inhabiting regions with mild marine or moderate continental climate where the number of frostless days is no less than 120 and the annual precipitation is about 500 mm. In Bulgaria they are most often encountered in mountain mixed and broadleaved forests.
3. Euxinic species – 19 species. This group of species occurs in the Crimea, Caucasus, the northern coast of Asia Minor and Turkish Thracia. In Bulgaria this complex is especially characteristic of the Black Sea coastal forests and the Istranja Mountains although some species have a wider distribution. As recent distribution and paleontology show, this group represents a relict of a rich subtropical forest fauna, which in the Neogene occupied vast areas of eastern Mediterranean regions.
4. Atlantic-Mediterranean species – 7 species. This small group is also composed, in general, of thermophilous forest mesophils, but as compared to the above group it differs in 2 peculiarities: a) a wider distribution in the Mediterranean region, with a spread of some species to the Atlantic coast of western Europe; and b) most species belong to families inhabiting, in general, the tropics. These facts and paleontological data enable us to regard these mollusks as relicts of the Paleogene.
5. Southern European mountain species – 10 species. These mollusks are distributed in the Atlas Mountains, mountainous regions of south and middle Europe and Anterior Asia (up to the Himalayas). They are inhabitants of limestone, i. e., they are calciphils and thermophils that under the conditions of the high insolation of southern regions enables them to live in all mountain zones.
6. Middle European species – 26 species. This group reflects the faunistic links between the Alps and the Carpathians. It consists of 3 subgroups: Balkan-Carpathian-Alpian (7 species), Balkan-Alpian (6 species) and Balkan-Carpathian (13 species). Among the mollusks of this group there are many calciphils living on rocks and hills (*Acicula, Abida, Argna, Macedonica, Laciniaria, Spelaeodiscus* and *Faustina*). The others are inhabitants of forest litter and upper soil layers. The group is collective in its origin. Side by side with species widely distributed in mountain regions of Europe and belonging to genera with analogous areas (*Vitrea, Oxychilus, Daudebardia* and *Carpathica*), there are species having a center of origin in the Alps (*Abida, Argna* and *Pagodulina*) or in the Carpathians (*Discus perspectivus, Spelaeodiscus triaria, Vestia riloensis*, etc.). Finally, this group includes mollusks of Balkan origin which penetrated the neighboring mountain areas (*Laciniaria, Macedonica* and *Faustina*).
7. Endemics of the Balkan Peninsula – 50 species and subspecies, most of which (44) occur only in eastern Balkans, i. e., mainly in Bulgaria. This is a result of a noticeable isolation of the malacofaunas of eastern regions from western malacofaunas. At present this isolation is supported by differences in relief, climate and vegetation between both parts of the Balkans. In the Miocene, this isolation was facilitated by the existence of a special arm of the Sarmat Sea, which passed along the drainages of the Vardar and Morava rivers.
8. Xerophils of anterior Asiatic origin – 16 species. This group includes all Enidae known for Bulgaria, excluding *Ena montana* and *E. obscura*, which belong to the European mesophils. Only 2 species in this group, *Zebrina varnensis* and *Chondrula macedonica*, are endemics of the Balkans. The other species are widely distributed in European and Asiatic Turkey, and belong to anterior

Asiatic genera. The appearance of these species in the Balkans is due to the increasing dryness of the climate, which began in the Miocene, and to continental connections with Anterior Asia (through Aegeide-land). In Bulgaria, these mollusks are quite common on the Black Sea coast and in the Thracian area. Only a few species in the whole country are distributed in xerothermic biotopes.

9. Xerophils of Mediterranean origin – 13 species. This group consists of only members of the Hygromiidae and Helicidae. As the members of the above group, these mollusks appeared in the Balkans due to the climatic aridization. However, they migrated not only from Asia Minor (species of the genus *Helix*), but also from other Mediterranean areas (*Helicella, Xeropicta, Monacha, Eobania*, etc.). The absence of Balkan endemics among these mollusks and the general distribution of corresponding genera speak in favor of an allochthonous origin of this group.

The steppe regions of Bulgaria (Lower Danubian, Black Sea and Thracian lowlands) go into the Steppe province of southeastern Europe of the Mediterranean subregion of the Palearctic region. Forest mountains and alpine areas of Bulgaria, together with the mountains of eastern Serbia and Mysian and the Macedonian hills, enter the eastern-Balkan district of the Balkan province of the European subregion of the Palearctic region.

The malacofauna of the Balkan province (i. e., without Greece, which together with its islands form a special province) is characterized by a high degree of endemism – out of 550 species nearly 50% are endemics. Excluding troglobionts, which are rather abundant in the Balkans, the other species are progressive endemics (terminology of Tolmachev, 1974). In this respect, the fauna in question resembles that of the Crimea, but differs from that of the Caucasus, whose significant part is composed of relict endemics of specific and generic status. This is a result of the greater isolation of the forest malacofauna of the Caucasus from other Mediterranean lands.

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ZOOGEOGRAPHIC ANALYSIS OF LAND MOLLUSKS OF NORTH TADJIKISTAN

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Abstract

As compared to South Tadjikistan, the malacofauna of the northern regions of the republic is poorly studied. The author's investigations (1967 to 1973) embrace 10 administrative regions of North Tadjikistan and contiguous regions of Kirghizia and Uzbekistan.

As a result, 63 species belonging to 26 genera and 13 families were established. For a zoogeographical analysis, 58 species were taken (2 introduced species and 3 of which the distribution is now little known, were not taken into account).

The terrestrial malacofauna is composed of 3 zoogeographic groups as follows.

A. Widely distributed boreal species (trans-holarctic and trans-palaearctic forms): 1, *Succinea elegans* Risso; 2, *Cochlicopa lubrica* (Müller); 3, *Vertigo antivertigo* Draparnaud; 4, *Pupilla muscorum* (Linné); 5, *Vallonia pulchella* (Müller); 6, *V. costata* (Müller); 7, *V. tenuilabris* (Al. Braun); 8, *Euconulus fulvus* (Müller); 9, *Zonitoides nitidus* (Müller); 10, *Deroceras laeve* (Müller). In respect to ecology, these mollusks are cold-resistant and hydrophilous (meso- and psychrophilic). That is why they inhabit biotopes with high and constant humidity – flood-plain forests, shores of waterbodies, spring bogs, humid leaf litter.

B. European-Asiatic mountain species: 1, *Truncatellina strobeli* (Gredler); 2, *Pupilla sterri* (Voith); 3, *P. triplicata* (Studer); 4, *Orcula doliolum* (Brug.); 5, *Pyramidula rupestris* (Draparnaud); 6, *Caecilioides acicula* (Müller); 7, *Phenacolimax annularis* (Studer). These mollusks occur in mountainous areas of southern and middle Europe and Asia Minor (up to the Himalayas). They are thermophilic and, to a certain extent, drought resistant species. They inhabit rocks and screens, especially limestones, or soils rich in lime. They are encountered from foothills to the alpine zone.

C. Endemics of Middle Asia: 1, *Pupilla signata* (Mousson); 2, *P. asiatica* (Moellendorf); 3, *Gastrocopta huttoniana* (Benson); 4, *Chondrulopsina chodschendica* Mukhitdinov; 5, *C. trisinuata* Mukhitdinov; 6, *C. intumescens* (Martens); 7, *Subzebrinus potaninianus* (Ancey); 8, *S. likharevi* Mukhitdinov; 9, *S. sogdianus* (Martens); 10, *S. secalinus* (Martens); 11, *S. albiplicatus* (Martens); 12, *S. errans* (Westerlund); 13, *S. liostracus* (Westerlund); 14, *S. kuschakewitzi* Ancey; 15, *S. diplus*

(Westerlund); 16, *Turanena martensiana* (Ancey); 17, *Pseudonapaeus miser* (Martens); 18, *P. castaneus* (Westerlund); 19, *P. subobscurus* (Ancey); 20, *P. trigonochilus* (Ancey); 21, *Sewertzowia drymaeus* (Westerlund); 22, *Macrochlamys turanica* (Martens); 23, *M. sogdiana* (Martens); 24, *M. retteri* (Rosen); 25, *M. schmidti* Brans; 26, *M. kasnakowi* (Westerlund); 27, *Parmacella roseni* Simroth; 28, *P. rutellum* Hutton; 29, *P. levanderi* Simroth; 30, *Bradybaena perlucens* (Rosen); 31, *B. lantzi* (Lindholm); 32, *B. fedtschenkoi* (Martens); 33, *B. semenovi* (Martens); 34, *Leucozonella retteri* (Rosen); 35, *L. ferganica* (Lindholm); 36, *L. cariodes* (Westerlund); 37, *L. mesoleuca* (Martens); 38, *L. angulata* (Westerlund); 39, *L.* sp. nov.; 40, *Euomphalia regeliana* (Westerlund); 41, *Xeropicta candaharica* (L. Pfeiffer). Most endemics are xerophils and inhabit xerothermic biotopes of all or some vertical zones. Some endemics belong to autochthonous genera or subgenera from Asia Minor (all Enidae, Nos. 34-41), others are of East Asiatic origin (Bradybaenidae, Nos. 30-33), and some endemics belong to tropical Indo-malayan genera (Ariophantidae, Nos. 22-26). It is clear that in the terrestrial malacofauna of North Tadjikistan endemics and subendemics of mountain areas of Middle Asia (41 species; 71.7%) prevail.

According to the general character of the malacofauna and to the abundance of Iranic-bactrian xerophils in it, North Tadjikistan (as well as South Tadjikistan) belongs to the Gyssaro-Darvaz district of the Afghano-Turkestan zoogeographical province (O. L. Kryzhanovskij, 1965).

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THE STRUCTURE OF SOME POLYMORPHIC SPECIES OF THE BRADYBAENIDAE FROM TIAN-SHAN

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Abstract

In previous investigations, the structure of the reproductive system and polymorphism of the shell of *Bradybaena lantzi* (Lindholm) and *B. plectotropis* (Martens) was determined. Some forms of *B. lantzi* with laeotropic shells were found. These live in isolated groups as well as in groups mixed with dexiotropic forms.

For control of morphological concepts of polymorphism, the same species and the same methods were used – the immunochemical reactions of double cross diffusion in agar gel and disc electrophoresis separation of esterases in polyacrylamide gel.

It was discovered that the composition of esterases in the laeotropic forms of *B. lantzi* differed from those in dexiotropic forms. Incidentally, it should be noted that interbreeding between the laeotropic and dexiotropic forms of terrestrial molluscs is impossible because of the location of the sexual openings. This fact, and the protein (esterase) differences, seem to be sufficient for confirming the theory and significance of a single mutation in the origin of new species. But, if we compare the values of differences between dexiotropic and laeotropic forms and differences between *Bradybaena lantzi* and a very close but "good" species (*B. plectotropis*) together with esterase active fractions of proteins, then we can see that the first fractions are considerably smaller. These differences appear because of only 1 specific fraction. In the latter case these differences appear because of many specific fractions and their specific systems.

Immunochemical methods demonstrate that the variations in forms of *Bradybaena plectotropis* (i. e., those with or without a band on the shell, with or without a pigmented foot epithelium, and with well expressed ribs on the shell) are genetically determinated. The ecologically produced rib form is most specific among some forms, but the value of this difference is much smaller than differences between each of the mentioned forms and *B. lantzi*.

Analogous data were obtained by using the disc electrophoretic method. A diversity between observed forms in *Bradybaena plectotropis* appears in fraction frequencies of esterase active protein, but differences between observed forms in *B. plectotropis* and *B. lantzi* demonstrate the presence of a specific fraction.

The population structure in *Bradybaena plectotropis* was determined by calculating the frequencies of esterase fractions and the frequencies of different forms of shell variability. All populations from coniferous forests differed from populations from hills, but populations of coniferous forests of various mountain ranges did not differ.

The elucidation of genotypic population structure of *Bradybaena plectotropis* is essential in studying the biology and epizoology of helmintosis.

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TERRESTRIAL MOLLUSKS OF THE CHELABINSK REGION AND PECULIARITIES OF THEIR GEOGRAPHICAL DISTRIBUTION

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Abstract

Until now the fauna of land mollusks of the Chelabinsk region has remained poorly studied. From 600 samples collected in 1970-73, there were recorded over 50 species belonging to 25 genera and 13 families. Forty-two species occur in the mountain forest zone, 41 species in the forest steppe and 33 species in the steppe zone. The species typical of the European part of the U. S. S. R. are dominant. In the mountain forest zone, there were found *Truncatellina costulata, Chondrula tridens* var. *major, Ena montana, Arion subfuscus, Bradybaena fruticum, B. schrenckі* and *Euomphalia strigella.* In the forest steppe and steppe zones, in addition to widely distributed species, there were found *Oxyloma dunkeri, Pupilla bigranata, P. triplicata, P. sterri* and *Chondrula tridens.* The latter species are characteristic only of forest steppe and steppe zones.

The malacofauna of the Chelabinsk region is formed by the following zoogeographical groups.

1. Palaearctic species: *Carychium minimum, Succinea putris, S. oblonga, Oxyloma elegans, Cochlicopa lubrica, C. nitens, Vertigo pygmaea, V. antivertigo, Columella edentula, Pupilla muscorum, Vallonia pulchella, V. costata, Punctum pygmaeum, Discus ruderatus, Nesovitrea hammonis, N. petronella, Aegopinella pura, Euconulus fulvus, Zonitoides nitidus, Vitrina pellucida, Deroceras agreste, D. laeve* and *Pseudotrichia rubiginosa.*
2. Species characteristic of European mixed and broadleaved forests: *Carychium tridentatum, Vertigo substriata, V. angustior, V. genesii, Truncatellina costulata, Ena montana, Trichia hispida* and *Bradybaena fruticum.*
3. Boreal species, i. e., the species occurring both in tundra and taiga of Europe: *Arion subfuscus.*
4. Species common to the mountain region of Middle Europe: *Pupilla sterri* and *P. triplicata.*
5. Siberian-taiga species: *Bradybaena schrenkі.*
6. Thermophilous species common to steppes and xerothermic biotopes of the forest zone: *Pupilla bigranata, Chondrula tridens* and *Euomphalia strigella.*
7. Relict of Tertiary times, which has a broken distribution area of widely spaced localities: *Gastrocopta theeli.*

Additionally, in some greenhouses of Chelabinsk were found 4 species introduced from southern regions of the country or from abroad: *Oxychilus cellarius, O. translucidus, Deroceras sturanyi* and *Boettgerilla pallens.*

Heterogeneity of the zoogeographic composition of the fauna is associated with a complex structure of the relief, climatic differences between natural zones of the region, peculiarities of soils and vegetation, and with increasing economic activities of man.

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FAUNA OF LAND AND FRESHWATER MOLLUSKS IN THE NEWLY DEVELOPED LANDS OF THE JAVAN VALLEY OF TADZHIKISTAN AND SOME REGULARITIES OF ITS FORMATION

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Abstract

The development and irrigation of lands are known to cause changes in biocoenoses. This paper concerns some moments in the formation of the molluscan fauna in newly developed lands of the Javan Valley of Tadzhikistan, which represents a valley of the synclinal type (the total area of 56.5 thousand ha.) situated between the Kara-Tau and Dzhetim Tau mountain ridges. In the south it adjoins the Vaksh Valley, which has absolute marks of 800 and 500 m above sea level in the north and south, respectively. By its climatic characters, it differs from other irrigated valleys of Tadzhikistan in the regime of atmospheric moisture: in the southern part of the valley precipitation accounts for an average of 450 mm a year, and in its northern part an average of 700 mm.

Investigations of the malacofauna of the Javan Valley biocoenoses were conducted during the period of 1971 to 1973. Many species of Enidae, Lymnaeidae, Physidae were subjected to quantitative analysis. Studies were carried out in adyrs (foothill badlands) on the slopes of mountains and ploughed fields used for cereal crops, in irrigated fields of cotton, lucerne and various vegetables, as well as in irrigation canals and footlands.

It was established that 3 species of xerophilic mollusks, *Subzebrinus sogdianus*, *Caecilioides acicula* and *Macrochlamys kasnakowi*, had inhabited Javan Valley up to its irrigation in 1967-1968.

In adyrs among vegetation and under stones in soil, 10 xerophilic species were found: *Pupilla signata*, *Subzebrinus sogdianus*, *S. kasnakowi*, *S. otostomus*, *Phenacolimax annularis*, *Macrochlamys kasnakowi*, *Leucozonella rufispira*, *L. retteri*, *L. mesoleuca* and *L. rubens*. The slopes of the mountains are also inhabited by xerophilic species, as well as *Truncatellina strobeli*. Here, under stones and stony screes, a calciphilic mollusk, *Bradybaena perlucens*, also lives.

Among vegetation along brooks and springs live, in general, psychro- and mesophilic species of land mollusks: *Oxyloma elegans*, *Cochlicopa lubrica*, *Pupilla muscorum*, *Vallonia pulchella*, *V. costata* and *Zonitoides nitidus*. Of these, *V. pulchella* and *V. costata* occur only in this region. Here, only in water, telmathobiontic species of freshwater mollusks occur: *Lymnaea* sp., *Physella acuta* and *Euglesa ovale*.

Due to irrigation, as a result of changes in the hydrothermic regime of soils (increase in humidity and decrease in temperature), xerophilic species are preserved only above irrigation ditches and in footlands of fields (cotton and other agricultural plants) where there are appropriate conditions for them. On the other hand, with the change in the water regime of soils, psychro- and mesophilic land species – telmalhobionts (inhabitants of small temporary or constant pools) and phytobionts (inhabitants of aquatic plants) – appear.

The land mollusk fauna of irrigated lands of the Javan Valley contains a hydrophilous slug introduced by man, *Deroceras caucasicum*, which is a serious pest of gardens in Tadzhikistan.

As a result of changes in the water regime of soils of a meadow type, more hydrophilic groups of invertebrates appear than was reported by many investigators (Giliarov, 1955, 1965; Valiakhmedov & Perel, 1962). Consequently, the fauna of land and freshwater mollusks of newly developed lands of the Javan Valley and neighboring regions consists of 27 species, 16 genera and 14 families. In connection with the development of irrigation agriculture, the former distribution areas of xerophilic species are reduced. Psychro- and mesophilic land mollusks penetrate along canals and irrigation ditches, while freshwater species are distributed with water.

Colonization takes place by species from neighboring adyrs and from slopes of mountains.

On newly developed lands, the terrestrial mollusk *Subzebrinus sogdianus* and the freshwater species *Lymnaea truncatula*, *L. auricularia persica* and *Physella acuta* are most abundant. A sharp increase, as compared to the initial biocoenosis, in the number of land mollusks was found.

Since mollusks are animals with a comparatively low mobility, the formation of the malacofauna on newly developed lands proceeds more slowly than with insects (Bei-Bienko, 1961) and requires several years.

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THE INFLUENCE OF TEMPERATURE AND MOISTURE OF THE UPPER SOIL LAYER ON THE HATCHING INTENSITY OF THE SLUG *DEROCERAS RETICULATUM* MÜLLER

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Abstract

The individual developmental cycle of any organism, including slugs, consists of a number of stages and is characterized by the availability of "critical" periods in their life (Dmitrieva, 1969). Consequently, a certain adequacy of requirements of organisms to climate takes place during their individual development.

The life of the field slug is closely connected with its environment. However, not all environmental elements are necessarily equivalent and equal. Some of them, such as temperature and humidity, directly affect biological processes; the others, such as soil, precipitation, wind and light, influence, first of all, temperature and humidity.

Since *Deroceras reticulatum* lays eggs in the soil at a depth of 2-3 cm, the most important of a whole complex of factors were taken during a study of the hatching intensity. These were (1) soil humidity at a depth of 3 cm, and (2) temperature of the upper 3 cm of the soil layer. While studying these factors, we used methods recommended by hydrometeorological posts and stations. The humidity was measured in percentages of the absolute dry weight of the soil. Each sample was taken 4 times at a depth of 3 cm. Sites of sampling were arranged in such a way that an average of these 4 repetitions reflected the soil humidity of the area under observation as a whole. The average percent humidity was calculated with an accuracy to 0.1%. Observations on the temperatures of the upper soil layer were conducted with an accuracy of 0.1°C. Measurements of temperature and humidity were regularly conducted each 7-10 days in definite sites, their area being equal to 5 m^2. At the same time, the calculation of slugs per 1 m^2 was undertaken. Since the slugs are night animals, calculations of their number were done at 6 to 7 A. M. In order to study the influence of temperature and humidity of the upper soil layer upon the hatching intensity of the field slugs under natural conditions, we used data from measurements and observations obtained during 3 years.

At first we'll consider the dependence of the hatching slugs (1st character) on the temperature of the upper soil layer (2nd character). For this purpose we use the methods of correlation analysis.

The calculation of the correlation coefficient is expressed by the following formulas:

$$r_{1,2} = \frac{\alpha_1 + \alpha_2 - \alpha d}{2\sqrt{\alpha_1 \cdot \alpha_2}} \pm \frac{1 - r_{1,2}^2}{\sqrt{n-1}}$$

$$\alpha = \Sigma v^2 - \frac{(\Sigma v)^2}{n}$$

where $r_{1,2}$ is the correlation coefficient; α is the sum of squares of central deviations; v is the variants of a given row; and n is the quantity of a row (the number of variants).

Substituting the values of the sums of squares of central deviations into the formula, we find that $r_{1,2} = -0.62 \pm 0.14$.

Taking into consideration a considerable value of the error of the correlation coefficient, it is necessary to determine the index of confidence ($t_{r_{1,2}}$). It is known that the confidence index of the correlation coefficient (t_r) for small samples can be estimated by a simple formula:

$$t_{r_{1,2}} = z\sqrt{n-3}$$

where z is a special index suggested by Fisher as being a function of the correlation coefficient. For our data, $t_{r_{1,2}} = 3.1$. An obtained confidence index suggests the correctness of our opinion, since for the majority of investigations in general biology, physiology and zoology, the confidence of the correlation coefficient equal to 2 is quite sufficient.

Thus, the obtained value of the correlation coefficient is quite confident and indicates the average reverse connection between the number of individuals per 1 m^2 and the temperature of the upper soil layer.

Correlation coefficients were estimated in the following way: (1) The number of individuals per 1 m^2 with its humidity of the upper soil layer (3rd character): $r_{1,3} = 0.69 \pm 0.11$; $t_{r_{1,3}} = 3.6$; (2) Temperature of the upper soil layer with its humidity: $r_{2,3} = -0.36 \pm 0.19$; $t_{r_{2,3}} = 1.6$.

The number of individuals was found to be connected on the average both with temperature and humidity of the upper soil layer at a rather high confidence of the correlation coefficient. Nevertheless, a

poor connection of soil temperature with humidity ($r_{2,3} = -0.36$) requires an additional study of these indices, since the value $r_{1,2}$ and $r_{2,3}$ can be affected by a poorly expressed correlation between temperature and humidity of the soil. Biometry gives us the possibility for investigating this problem by means of partial correlation coefficients.

Let us consider, at first, the connection between the number of individuals per 1 m^2 and temperature of the upper soil layer, the effect of soil humidity (constant value) being excluded. This connection can be expressed by the formula of the partial correlation coefficient:

$$r_{1,2\cdot3} = \frac{r_{1,2} - r_{1,3} \cdot r_{2,3}}{\sqrt{(1 - r_{1,2}^2)(1 - r_{1,2}^2)}} = 0.51$$

The independent connection between the number of individuals per 1 m^2 and soil humidity (the effect of temperature is excluded) can be expressed by the formula:

$$r_{1,3\cdot2} = \frac{r_{1,3} - r_{1,2} \cdot r_{2,3}}{\sqrt{(1 - r_{1,2}^2)(1 - r_{2,3}^2)}} = 0.64$$

The obtained partial correlation coefficients are very important, since they confirm the presence of the independent average connection between the number of individuals per 1 m^2 and the temperature and humidity of soil, with a leading role of the humidity factor.

Since the temperature and humidity are vitally important factors for slugs, it is expedient to study a joint influence of these factors upon their number. It can be expressed by the coefficient of multiple correlation:

$$r_{1,2,3} = \sqrt{\frac{r_{1,2}^2 + r_{1,3}^2 - 2(r_{1,2} \cdot r_{1,3} \cdot r_{2,3})}{1 - r_{2,3}^2}} = 0.80$$

Thus, a joint effect of the temperature and humidity of the soil on the numbers of the pest is expressed rather clearly, i. e., proved by a high correlation coefficient (0.80).

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LIFE CYCLES AND DAMAGE CAUSED BY THE SLUGS *DEROCERAS CAUCASICUM* (SIMROTH) AND *PARMACELLA RUTELLUM* HUTTON IN THE ALMA-ATA REGION (KAZAKH SSR)

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Abstract

Seven species of slugs which are pests of floral and vegetable cultures are reported from the Alma-Ata region. These are *Parmacella rutellum* Hutton, *Deroceras agreste* (Linnaeus), *D. altaicum* (Simroth), *D. laeve* (Müller), *D. caucasicum* (Simroth), *D. sturanyi* (Simroth) and *D. reticulatum* (Müller). The 3 latter species were apparently introduced into this region from the Caucasus and the European part of the U. S. S. R. Most injurious are *Deroceras caucasicum* and *Parmacella rutellum*. The knowledge of their biology is quite necessary for an elaboration of control measures against them. *Deroceras caucasicum* occurs in all natural zones, except that they desert one; *P. rutellum* is found only in the foothill zone. It is in this zone that both slugs are most injurious. Thus, the loss in crops caused by *D. caucasicum* amoúnted to 37% for tomatoes, 43% for cucumbers and 50% for strawberries.

Both species of slugs have a 1-year life cycle, but *Parmacella rutellum* differs from *D. caucasicum* in having a summer diapause. The life cycle of *P. rutellum* has the following stages: spring (April–June) is the period of most intensive growth and oviposition, ending in the death of adult slugs; summer (July–August) – hatching of young and aestivation; autumn (August–October) – awakening and growth of yearlings; winter and beginning of spring (November–March) – hibernation of young slugs. Therefore, the injurious effect of *P. rutellum* is most intensive in autumn, spring and beginning of the summer. In May–June, they cause great damage to seedlings of peppers, eggplants and tomatoes. At the end of June, adult *P. rutellum* (60–68 mm in length) lay 10 to 80 yellowish eggs (3.1–4.3 mm). The hatching of young takes place on the 25th–30th day. The young slugs have an amber-colored shell (length of body –

5.2 mm, length of shell – 3.2 mm). In 3–4 days, young slugs, despite the optimal humidity and temperature, bury themselves in the soil, pull the body into the shell and cover its aperture with a provisional operculum.

The life cycle of *Deroceras caucasicum* has the following stages: in autumn some slugs die after oviposition; in winter, eggs, adult and young slugs hibernate; in spring (April–May), adult slugs lay eggs and die after that, last year's slugs grow and new young appear; in summer, yearlings grow and overwintered young slugs lay eggs.

In the foothill zone of the Alma-Ata region, *D. caucasicum* has not less than 3 generations a year, and up to 6 generations under laboratory conditions. So the slugs are most injurious in the summer and autumn. In June, they injure strawberries and seedlings of cucumbers, peppers and tomatoes; in July to the middle of October, the slugs injure cabbage, fruits of tomatoes and cucumbers.

Temperature and humidity are important factors for both adult and young slugs, and for the development of their eggs. The slugs are active at an air temperature of 11.6–24.8°C, a soil temperature of from 8–19.4°C, and a relative humidity in the air of 47.5–69%. Relative humidity of air lower than 45% and humidity of soil lower than 18% inhibit the activity of the slugs. They go deep into cracks in the soil, or hide themselves at the base of plants and under clods on the ground.

During the day, *D. caucasicum* is most active at an air temperature of 15–24.8°C, a soil (20 mm depth) temperature of 13.6–19.4°C and a relative humidity in the air of 54–64%. However, some cases were recorded when slugs were active at an air temperature of 24–28°C, a soil temperature of 19–24°C, and a relative humidity in the air of 54–64%, provided that soil was humid enough and juicy food was available. Such figures have been reported for no other slugs.

Deroceras caucasicum is very voracious, with the exception of the early spring and the oviposition period. Its feeding intensity depends on temperature, its optimum ranges being from 15–21%. Fifty-to-60-day-old slugs are most voracious. One individual (26 mg in weight) can eat 13 mg of cucumber leaves, 7.8 mg of tomato leaves, 7 mg of cabbage, 4.4 mg of eggplant, or 5.2 mg of pepper a day. Ninety-six-day-old slugs (132 mg) eat 21 mg of cucumber leaves, or 15.8 mg of tomato leaves a day. Their daily increase in weight reaches 30 mg. Adult slugs are also very voracious (1 individual can weigh 135–334.6 mg).

The time of embryogenesis and growth of *Deroceras caucasicum* also depends on temperature. The survival rate of eggs at different air temperatures varies. At 15–18°C and under conditions of optimal humidity, 70–95% of the individuals hatch. If the temperature is lower or higher, the percent hatching decreases.

Eggs develop at different times. The difference between the appearance of the first slugs and the last ones is 1–20 days at temperatures of 15–18°C. A temperature of 15–20°C is optimal for growth.

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A STUDY OF LAND MOLLUSCS WHICH ARE INTERMEDIATE HOSTS OF PROTOSTRONGILID HELMINTHS IN DIFFERENT VERTICAL ZONES OF AZERBAIJAN

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Abstract

Since 1971 studies have been carried out on natural infection of land mollusks with larvae of protostrongilid parasites in the main landscape geographical zones of Azerbaijan: lowland (subzone: the Kura River regions with irrigated agriculture), foothill (subzone: foothills of Caucasus Minor at the Kura-Arax lowland), mountain (subzone: high-mountain areas of Caucasus Minor. In all, 16,250 specimens of land snails and slugs belonging to 9 families, 17 genera and 22 species were investigated for natural infection with larvae of protostrongilids.

The most abundant species on pastures of the lowland zone were *Xeropicta derbentina* and *Chondrula tridens*. The larvae of protostrongilids were found only in *X. derbentina* (10.6%), the infection intensity being 1–2 specimens.

In the region of the foothill zone, 15 species of mollusks were investigated (*X. derbentina, Euomphalia pisiformis, E. ravergiensis, E. selecta, Xerosecta crenimargo, Helix lucorum taurica, Physospira albescens, Levantina djulfensis, C. tridens, Imparietula pupoides, Orcula doliolum, Pomatias rivulare, Vallonia costata, Parmacella ibera* and *Deroceras caucasicum)*. From these species, only 3 (*P. rivulare, O. doliolum*

and *L. djulfensis*) had no protostrongilid larvae. The main intermediate hosts of protostrongilids in the foothill zone were *X. derbentina, X. crenimargo, E. pisiformis, H. lucorum taurica* and *D. caucasicum*. The infection rate of species sometimes can reach 31.3%. The infection intensity of mollusks here varies from 1 to 22 specimens.

In the mountain zone, 21 species of mollusks were studied for infection with protostrongilid larvae. These species include those from the foothill zone (excluding *L. djulfensis*) and *Cionella lubrica, Jaminia isseliana, Napaeopsis hohenackeri, Euxina somchetica, E. tschetschenica, Hesseola solidior* and *Fruticocampylaea narzanensis*. Larvae of protostrongilids were found in 15 species: *H. solidior, F. narzanensis, N. hohenackeri* and *J. isseliana*, and in the other 11 species serving as intermediate hosts of protostrongilids in foothill areas. Of mollusks infected with larvae of these helminths, the main part in the transmission of the infection in the mountain zone belongs to *Xeropicta derbentina, X. crenimargo, D. caucasicum, Physospira albescens, Euomphalia selecta, N. hohenackeri, Helix lucorum taurica, E. pisiformis* and *Parmacella ibera*. On summer pastures, the infection of some species of mollusks with protostrongilid larvae was up to 42.0%, the infection intensity being 1 to 32 specimens.

These studies show that a distinct landscape-vertical zonality exists in the distribution of land mollusks and their infection with protostrongilid larvae.

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RESULTS OF STUDIES OF FRESHWATER MOLLUSKS FROM THE NORTHERN PART OF WESTERN SIBERIA

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Abstract

During the period of 1970-73, 300 different waterbodies were investigated in the drainage of the Lower Ob, and in the Jamal, Taz and Gydan peninsulae. Eight hundred samples of benthos were taken, including 400 quantitative samples. In addition, mollusks found in 300 stomachs of pelyad, broad whitefish, Siberian powan, muksun and ide were taken into account.

In waterbodies of Western Siberia, 65 species of mollusks were found, of which 5 species (*Euglesa obensis, E. jamalensis, E. gydanensis, E. novicovi, Neopisidium johanseni*) were described as new. Fourteen species (*Valvata klinensis, Bithynia contortrix, Lymnaea terebra, Sphaerium capiduliferum, Musculium johanseni, E. suecica, E. globularis, E. scholtzi, E. cor, E. tetragona, E. nordenskioeldi, E. talievi, N. odhneri* and *N. alpinum*) were recorded for the first time for Western Siberia. The freshwater mollusks belonged to 17 genera (*Valvata* with 6 species, *Bithynia* with 3, *Lymnaea* 9, *Physa* 1, *Sibirenauta* 1, *Planorbarius* 3, *Planorbis* 1, *Anisus* 6, *Choanomphalus* 1, *Sphaerium* 4, *Amesoda* 1, *Sphaerinova* 1, *Musculium* 2, *Lacustrina* 1, *Pisidium* 1, *Euglesa* 20 and *Neopsidium* 3).

The waterbodies can be divided into 4 biological-productional types on the basis of their specific composition and the quantitative development of the whole zoobenthos and, in particular, the mollusks. Fourteen species live in rivers (*Valvata confusa, Amesoda asiatica, Sphaerinova inflata, Musculium creplini, M. johanseni*, etc.), their density is 2,200 specimens/m^2 and their biomass 69.5g/m^2. Forty-three species were recorded from tributaries of the rivers, their greatest quantity amounting to 12,000 specimens/m^2 and their biomass to 200 g/m^2. Fifty-one species were found in floodplain lakes, their quantity reaching as much as 2,040 specimens/m^2 and their biomass to 15.4 g/m^2. Twelve occurred in extra-valley lakes, their greatest quantity amounting to 500 specimens/m^2, with a biomass of 3.4 g/m^2.

In regard to the effect of currents on the occurrence of definite mollusk species in a particular type of waterbody, the malacofauna of the northern part of Western Siberia can be arranged into 2 ecological groups – reobionts (11 species) and stagnobionts (50 species). Reobionts are represented by psammophils (*Pisidium amnicum*), pelophils (8 species) and by psammopelophils (*Valvata confusa, Amesoda asiatica*). Stagnobionts include limnobionts (40 species) and telmatobionts (10 species). Limnobionts are represented by phytophils (15 species) and psammopelophils (7 species). The group of telmatobionts is represented by phytophils (7 species) and pelophils (*Lymnaea auricularia, L. eversa* and *Euglesa globularis*). The composition of ecological groups of mollusks is somewhat unstable, since many species inhabit contiguous biotopes.

Mollusks are valuable for benthophags and play a major part in the feeding of pelyad, broad whitefish, Siberian powan, muksun and ide. The general frequency of occurrence of mollusks in food of these fish varied from 52.5 to 85.5% (in the pelyad, 2.4%). Of the mollusks inhabiting northern waterbodies of Western Siberia, 38 species were found in the food consumed by fishes. The frequency of occurrence of several species as food was as follows: *Valvata confusa* (45.4%), *Bithynia troscheli* (87.5%), *Lymnaea terebra* (50%), *L. palustris* (30%), *Planorbis planorbis* (40%) and *Amesoda asiatica* (36.4%).

In regard to zoogeographical considerations, the malacofauna had a mixed composition, which included Euro-siberian elements (26 species; 40%), Siberian elements (21 species; 32.3%), Euroasiatic (12 species; 18.4%), Asiatic (2 species; 3.1%) and Holarctic elements (4 species; 6.1%).

According to the accepted system of malacogeographical regions (Starobogatov, 1970; Novikov, 1970), the northern part of Western Siberia should be referred to the Lower Ob province of the European-Siberic subregion of the Palearctic. In turn, the province is subdivided into the following districts: the Lower Ob (drainage of the Lower Ob northward to the Polar Circle) with its left (54 species) and right bank subdistricts, and the Transpolar peninsulae, where 37 species of mollusks occur. The malacofauna of the Lower Ob district gravitates to the European and West-siberian faunas; that of the Transpolar district gravitates to the East-siberian fauna. The fauna of the Lower Ob, when combined with the total fauna of the Lower Ob and the basin of the Middle Ob, accounts for 63.1% (42 species) of the fauna; when combined with the Lower Yenisei fauna, it accounts for 53.8% (35 species) of the fauna; when combined with the Irtish basin, it accounts for 50.8% (33 species); and when combined with the Pechora basin, it accounts for 40% (26 species) of the fauna.

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FRESHWATER MOLLUSKS AND THE DIVISION OF THE PECHORA DRAINAGE

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Abstract

The freshwater mollusk fauna of the Pechora drainage consists of 50 species, belonging to 18 genera and 8 families. In the European-Siberian subregion, the Pechora drainage, together with the coast of the Pechora Sea, is regarded as a province (Starobogatov, 1970). Forty species of mollusks, the distributions of which have been precisely established, were used for the sub-division of the drainage. The systematic and geographic analyses have enabled us to divide the province into 5 malacofaunistic districts. In each district there was found a species not recorded from other districts: in Upper Pechora, *Segmentina complanata*; in Middle Pechora, *Sphaerinova inflata*; in Lower Pechora, *Planorbis carinatus*; in Maritime-Pechora, *Anisus lencostoma*; and in Usa, *Lacustrina dilatata*. The total number of species established for each district was 36, 37, 34, 29 and 37, respectively; the numbers of species taken for analysis were 29, 28, 29, 26 and 30, respectively. The index of difference between these districts, defined by Preston's method, varies from 0.28 to 0.35. The Maritime-Pechora district includes the Pechora delta and tundra rivers running into the Pechora Sea. In the province, the number of members of the Planorbidae decreases from south to north, while members of the Pisidiidae increase in number, on account of species of the genus *Euglesa*.

Over 1,200 hydrobiological benthic samples and about 200 samples of food used by mollusk-eating fishes collected in 1952-72 were taken for the ecological-geographical division of the Pechora drainage. More than 25,000 specimens, excluding undetermined *Euglesa*, were used. After the analysis, 10 malacological districts were separated. Of these 2 (the Ural and Timan districts) include rivers of the mountains and foothills, 3 regions include lake-river systems and the delta situated in the Bolshezemelskaja and Malozemelskaja tundra, and the other 5 regions include the plains parts of the Pechora and its main tributary, the Usa, in the taiga zone. The Lower Pechora is characterized by an intensive erosion of its banks, a shifting sandy bottom, and, due to this, by the lack of macrophytes in the river bed (Zvereva, 1969).

In the Ural, Timan and Upper- and Middle Pechora districts, as well as in large lakes of the eastern part of the Bolshezemelskaja tundra, *Lymnaea ovata* and *Anisus acronicus* prevail (55-69%). They occur in the thickets of macrophytes, on algae-covered stones, and on silt-covered pebble and detritus deposits.

In the district of the Pechora and Usa confluence, *Amesoda asiatica* is most abundant (30%). Further north, in the Kosju-Usa district, *Valvata piscinalis*, which is pelo- and phytophil, dominates (53%). This district, as well as the Pechora-Usa, and the Middle and Upper Pechora districts, are confined to hollows of interglacial lakes of the Cis-uralian chain (Zvereva, 1969). In the Lower Pechora district, *Pisidium amnicum* occurs, preferring parts with a slow current and sand slightly covered with silt.

In the above districts, separated on the basis of the prevailing type of biotope and the dominant species complex, the occurrence of mollusks in samples taken from the river bed ranges from 3% (in the Lower Pechora) to 65% (in Timan). In the kurjas (river bays) and lakes associated with the bed, the number of mollusks is never lower than 70%. The greatest density and biomass of mollusks are reported from the Soiva River (in Timan): 26.4 thousand specimens/m^2 and 1.6 kg/m^2 in a small lake connected with the river, on silt-covered sand with moss foulings; 12.6 thousand specimens/m^2 and 517 g/m^2 in a shoal of the river on stones covered with moss. The Middle Pechora district has the next largest density – 160 g/m^2. In some biotopes, the zoobenthos biomass is represented only by mollusks; but, the part of mollusks varies, on the average, from 6.2% (in the Ural district) to 45% (in the Middle Pechora district).

The average density and biomass are mostly low in the Ural rivers; these rivers are characterized by rapid currents and poor mineralization of the water (up to 100 mg/1). Their mollusk colonies are low in density and biomass – 30 specimens/m^2 and 300 mg/m^2; and with allowance for their occurrence – 4 specimens/m^2 and 24 mg/m^2.

The highest of the density and biomass indices, due to the Soiva River, are in the Timan district: over 1 thousand specimens/m^2 and 7 g/m^2 in mollusk colonies, and over 500 specimens/m^2 and 3 g/m^2 as estimated for the whole bottom square. It is possible that in the future the Timan mountain ridge will be divided into malacological districts (or subdistricts) due to differences between its parts in the level of overgrowing, silt accumulation and the degree of mineralization of the surface waters: up to 250, 400 and 800 mg/l (Vlasova, 1965).

If the Ust-Voisk water reservoir on the Pechora is constructed, it would occupy the main territory of the Upper and Middle Pechora districts. Under these circumstances, reophilous species will disappear and eurybionts and limnophilous species will increase in number. At the same time, an increase in the number of ide, roach and perch should be expected. Several species of trematodes were recorded from these fishes; the intermediate hosts of these parasites are mollusks. Thus, in addition to the unfavorable after-effects of the water reservoir, from the construction there would be, as noted by ichthyologists, a possible rise in the degree of infection, which should be taken into account.

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CONTENTS AND ZOOGEOGRAPHICAL ANALYSIS OF THE FRESHWATER MALACOFAUNA OF THE TEREK DRAINAGE

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Abstract

Available data on the malacofauna of waterbodies of the Terek drainage were rather scanty; previous to this study only 19 species were reported. As a result of studies of material collected in 1962-72, 49 species of freshwater mollusks can now be reported for the Terek drainage. These mollusks belong to 21 genera and 9 families. The Gastropoda are represented by 32 species (65.3% of the total), the Bivalvia by 17 species (34.7%). Of the Gastropoda, the most numerous were the Pulmonata, with 30 species (93.8%); the other 2 species (6.2%) belong to the Pectinibranchia. Thirty species are recorded from the Terek drainage for the first time, e. g., *Physella acuta* (Draparnaud), *Planorbis carinatus* Müller, *Anisus acronicus* (Férussac), *Armiger crista* (Linnaeus), *Unio pictorum* (Linnaeus), *Anodonta cygnea* (Linnaeus), *Euglesa hibernica* (Westerlund), *E. subtruncata* (Malm), *E. milium* (Held) and *E. personata* (Malm). Sixteen species are new for the fauna of the Caucasus: *Lymnaea taurica* Clessin, *Planorbis sieversi* Mousson, *Armiger bielzi* (Kimakowicz), *Hippeutis euphaea* (Bourguignat), *Thedoxus pallasi* Lindholm, *Valvata cristata* Müller, *Unio longirostris* Rossmaessler, *Anodonta subcircularis* Clessin, *A. ponderosa* C. Pfeiffer, *Amesoda scaldiana* (Normand), *Sphaerium nucleus* Studer, *Musculium hungaricum* (Hadzi), *M. creplini* (Dunker) and *Dreissena polymorpha* (Pallary). Six species are first reported for the U.S.S.R.: *Lymnaea corviformis*

Bourguignat, *Hippeutis diaphanella* (Bourguignat), *Ancylus capuloides* Porro, *Segmentina montgazoniana* (Bourguignat), *S. caucasica* Kazannikov, and *Odhneripisidium terecense* Kazannikov; the latter 2 are new to science.

In considering the zoogeographical peculiarities of this malacofauna, its mixed nature should be noted. This is associated with the fact that the species belong to several groups. These groups are: the widely distributed Holarctic and Palaearctic species – *Lymnaea auricularia, L. stagnalis, L. peregra, L. truncatula, Aplexa hypnorum, Physa fontinalis, Anisus acronicus, Armiger crista* and *Musculium creplini*; the European-Siberic species – *Planorbis planorbis, Anisus albus, Acroloxus lacustris, Amesoda scaldiana* and members of the genera *Segmentina, Hippeutis, Anodonta* and *Euglesa*; the European species – *Lymnaea taurica, L. corviformis, Planorbis carinatus, P. philippianus, Anisus vorticulus* and members of the genera *Ancylus* and *Unio*; the Ponto-Caspian-Aral species – *Theodoxus pallasi, Dreissena polymorpha*; the Mediterranean species – *Physella acuta*; and the Asiatic species – *Planorbis sieversi* and a member of the genus *Odhneripisidium*.

A distinct connection with the Volga and Ural drainage areas can be detected in the malacofauna. But, on the other hand, a number of species and larger taxonomic units characteristic of the Volga-Ural province are absent from the Terek drainage. They are members of the genus *Planorbarius*, and the families Viviparidae, Bithyniidae and Valvatidae (excluding *V. cristata*). The specificity of the structure of the malacofauna suggests the separation of the Terek district as a distinct zoogeographical unit of the Volga-Ural province. The diversity of distribution areas, the heterogeneity of the malacofauna of the Terek drainage, the distribution of mollusks in the vertical zones, and palaeogeographical data enable the Terek district to be divided into 2 parts, a lowland-delta part (East Ciscaucasian) and a foothill-mountain (northern slopes of the Central Caucasus) part.

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REGULARITIES IN THE FORMATION OF THE MALACOFAUNA IN ESTUARIES OF THE DNIEPR, BUG AND DNIESTER RIVERS

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Abstract

Changes in the hydrological regimes of estuarine regions of the northwestern Black Sea area, as a result of dam construction and progressive reduction in the outflow of rivers, have led to considerable variations in the composition and distribution of the malacofauna of the above regions. Mollusks, as in former times, occupy a dominant position in the formation of their hydrobiological regime; however, we can state that great changes have taken place in the areas of distribution of their populations, i. e., a reduction, and in a number of cases a complete disappearance, of a part of their genofund.

Despite the specificity of the ecosystems in question, there were noted general regularities in the formation of invertebrate populations inhabiting their aquatoria. They depend, first of all, on changes in mineralization in biotopes along the longitudinal and transverse axis of limans, the character of bottom deposits and the wave activity of shallow coastal areas. This results in the successive change from colonies of euryhaline Mediterranean-Atlantic forms and other immigrants of the estuarine coast to colonies of marine Ponto-Caspian forms which have adapted to the opposite end of the saline ecological spectra in polyhaline regions of limans. They are replaced by colonies of genetically euryhaline freshwater and relict forms of aquatoria of heterohaline zones of the central regions of the limans. They, in turn, are replaced by freshwater and Caspian faunas in oligohaline regions of the upper parts of the limans and in the lower reaches of the rivers in channels, where reophily replaces salinity as a main limiting factor for the fauna of the limans. The same regularities are common, to a certain extent, in the composition and distribution of meroplankton (which is formed by mollusk larvae and zooplankton, composing 0.7 to 1.3% of the average annual reserves in these waters).

The planned water regulation stipulated in estuarine regions must make provision for a certain salinization of these areas, so that they will be maintained as running waterbodies for preserving their unique plants and animals, including the malacofauna.

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SOME RESULTS OF THE STUDIES OF MOLLUSKS FROM WATERBODIES OF THE DNIESTER DRAINAGE

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Abstract

During the period 1967-73, studies were carried out in waterbodies of different ecological types in the Dniester River drainage. In all, 1,131 hydrobiological samples were collected: 488 qualitative and 643 quantitative samples. The work was done in order to establish the specific composition of the mollusk fauna, to determine the distribution of the mollusks in regard to the various biotopes, to study dynamics of development of the mollusks in regard to concrete ecological conditions of the habitat, and to ascertain the role of mollusks in nature. The previous data available were very scanty and insufficient to give a complete picture of the freshwater malacofauna of the Dniester drainage.

According to our data, this fauna includes 78 species (52 gastropods (66.6% of the malacofauna) and 26 bivalves (33.4%)), which belong to 15 families (Neritidae, Viviparidae, Valvatidae, Bithyniidae, Lithoglyphidae, Pyrgulidae, Melanopsidae, Lymnaeidae, Physidae, Bulinidae, Planorbidae, Unionidae, Dreissenidae, Pisidiidae and Cardiidae) and 36 genera. Among the families, the Planorbidae rank first in the number of species (13 species), followed by the Unionidae (10 species) and the Pisidiidae (10 species). The genus *Anisus* had the most species (7), followed by *Turricaspia*, *Lymnaea* and *Euglesa*.

The malacofauna of the waterbodies of the Dniester drainage can be grouped into rheobionts and stagnobionts. The most distinct rheophily was observed in *Theodoxus fluviatilis*, *T. danubialis*, *T. transversalis*, *Viviparus viviparus*, *Unio pictorum*, *U. tumidus* and *Crassiana crassa*. The rheobionts are represented by litho-rheobionts, psammo-rheobionts, pelo-rheobionts and phyto-rheobionts, while stagnobionts are represented by pelo-psammobionts and phytobionts. However, edaphopathy of the malacofauna, as well as of the other hydrobionts of the Dniester fauna, is often disturbed due to inconstancy of the hydrological regime.

The largest number of species and subspecies was recorded from flood-land waterbodies (47 species or 60.2% of the total malacofauna) and the minimum number (20 species or 38.8%) from the tributaries of the Dniester.

Thirty-five species inhabit the Dniester River itself; this is nearly a half of the total drainage malacofauna. The greatest number of forms (33 species or 94.2%) occurs in the lower part of the river. *Theodoxus fluviatilis* (343 specimens/m^2, with an occurrence frequency of 46.2%), *Dreissena polymorpha* (862 specimens/m^2; 48.9%) and *Lithoglyphus naticoides* (531 specimens/m^2; 43.6%) were most abundant.

In the middle part of the Dniester, the number of species decreased (to 24), but this was accompanied by an increase in the average density or frequency of occurrence of some species. A great increase in the quantity as compared to the lower reaches is observed in *Viviparus viviparus*, *Bithynia tentaculata*, *Fagotia acicularis* and *Sphaeriastrum rivicola*. Twenty-one species are reported from the Dubossar Reservoir, where both stagnobionts and rheobionts occur. The malacofauna of the upper portion of the Dniester is poorer, not only in composition (21 species), but also in number.

In the foothill zone, *Theodoxus fluviatilis*, *T. danubialis*, *Viviparus viviparus*, *Crassiana crassa*, etc., are very abundant. *T. fluviatilis* has a very great density here, 2,520 specimens/m^2, the average number being 138 specimens/m^2.

From a zoogeographical point of view, the malacofauna of the Dniester drainage is rather diverse. It is formed by Palaearctic (13 species; 16.8%), European (25 species; 32.4%), European-Siberian (18 species; 23.3%), Ponto-Caspian (19 species; 24.3%) and Mediterranean (2 species; 2.5%) groups.

Mollusks of the Dniester drainage were found in stomachs of such fishes as the Dnieper barbel (58% occurrence), vimber (50%), European catfish (40%), bleak (25%), common carp (23%), carp-bream (18%), etc.

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ON THE ORIGIN OF THE "CASPIAN" MOLLUSK FAUNA IN ESTUARIES OF THE NORTHWESTERN BLACK SEA

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Abstract

The brackishwater mollusk fauna of Black Sea estuaries has been evolving for a considerable amount of time. A prototype of the Ponto-Caspian fauna developed in the Pannonian brackishwater basin (Andrusov, 1897). In the Pontian period, as a result of migrations from the Pannonian and Aegean basins to the Black Sea-Caspian basin, a special type of fauna (called a Pontian type by N. I. Andrusov) was formed, which developed up to the Kujalnikan age. The northwestern part of the Kujalnikan Sea was inhabited by mollusks very close to and sometimes identical with Recent Ponto-Caspian estuarine mollusks. The Recent Caspian fauna was formed initially as 2 diverse faunas: one in the Caspian basin (by means of changes in the Akchagylian fauna), and the other in the Black Sea basin (from descendants of the Pontian fauna). In the Tchaudian and especially in the Old-Euxinian epochs, due to a connection of the Euxinian basin with the Caspian Sea, a mutual migration of mollusks took place (Eberzin, 1955; Starobogatov, 1970). However, the main nucleus of the malacofauna was composed of local species.

The migration of Mediterranean mollusks (which began as far back as the Old-Euxinian time and was due to established connections with the Mediterranean Sea) resulted in the displacement of the brackishwater fauna into the northwestern part of the basin, which had undergone a considerable freshening due to rivers such as the Danube, Dniester, Dnieper and the South Bug. The distribution of brachishwater mollusks was reduced a great deal during the Karangatian transgression. But even at that time the brackishwater fauna was not completely destroyed, as the adherents of the migration theory assume. Most convincing examples are materials from the Dnieper and the Danube (Goretzky, 1970; Litianu et al., 1963), which, in the same age, deposits were found containing typical Karangatian mollusks and the most recent estuarine forms. The regression which took place at the post-Karangatian time and the isolation of the Euxinian basin resulted in its freshening and the development of mollusks which had originated from limans and mouthes of the rivers.

The composition of the mollusk fauna of the New-Euxinian basin has been sufficiently studied (Nevesskaya, 1963, 1965; Ilina, 1966; Golikov & Starobogatov, 1966, 1972). We should like to emphasize the following. Many species of the New-Euxinian basin are relicts of the Old-Euxinian and even Kujalnikan basins. They are as follows: *Monodacna colorata* (Eichwald), *Hypanis dolosmiana* (Borcea), *Dreissena caspia crassa* (Andreae), *D. rostriformis bugensis* (Andreae), *Micromelania caspia lincta* Milach., *M. dybowski* Milach., *Theodoxus pilidei lamelliferus* Milach. and *T. euxinus* (Clessin). It should be noted that the list does not include some endemics of the Azov-Black Sea basin described by Golikov & Starobogatov (1966). But even the included species are enough to be convincing that there is a prevalence of Euxinian species over Caspian immigrants in the New-Euxinian basin, which suggests only a small faunistic exchange in pre-New-Euxinian and partially at New-Euxinian time.

It is noteworthy that the mollusk faunas of the New-Euxinian basin, of the ancient Black Sea and of Recent limans are practically identical. At the end of the New-Euxinian time, a connection with the Mediterranean Sea was restored and a gradual rise of the sea level naturally took place, together with its salinization and the migration of brackishwater mollusks into limans and estuaries. Since that time and up to now, their development has been limited by estuarine systems.

Thus, the brackishwater fauna of the Old-Euxinian type was not destroyed completely by any increases in salinity; changes took place only in its distribution and localization in estuarine systems. The presence of common or close species in limans of the Black Sea coast and in the Caspian Sea is a result of migrations of mollusks during Tchaudian, Old-Euxinian and New-Euxinian times. Low endemism in the molluscan fauna of the Azov-Black Sea basin is the main argument in favor of the migration theory (Mordukhae-Boltovskoy, 1946, 1960), but it is not confirmed by facts. According to the data of Golikov & Starobogatov (1966), 11 of 18 species of brackishwater gastropods are endemics of the Azov-Black Sea basin, and only 7 are identical to Recent Caspian species or are their subspecies. If bivalve endemics are added to this number, it will become clear that the brackishwater molluscan fauna in estuaries of the Black Sea are relict rather than migrational species. It would be correct to call it a Ponto-Caspian fauna, but not a "Caspian" fauna, which would emphasize its genetic essence. A characteristic feature of Ponto-Caspian mollusks is their high viability and wide ecological plasticity, which has been developed under conditions of extremely changeable hydrological and salt regimes.

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MALACOFAUNA OF THE DNEPRODZERZHINSK RESERVOIR

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Abstract

The upper part of the Dneprodzerzhinsk water reservoir is formed by sand biocoenoses inhabited mainly by mollusks of the genera *Sphaerium, Pisidium* and *Dreissena*.

The fall in the speed of the water flow results in silting of the sandy bottom. The bottom of the middle part of the reservoir is covered with moderately silted sand, which is inhabited, in general, by a pelophilic fauna with 3 main groups of invertebrates – tubificids, chironomid larvae and mollusks. Among the mollusks, the most abundant are *Dreissena polymorpha* and *D. bugensis*. Their number and biomass amount to 25,000 specimens/m^2 and 7,650 g/m^2 respectively. The middle part of the reservoir, as well as the Poljansky and Vorskljansky bays, is characterized by the richest (both qualitatively and quantitatively) bottom fauna.

On the silted sands of the lower part of the reservoir where the water current is very slow, the bottom fauna – at depths up to 10 m – consists of tubificids, chironomid larvae and mollusks (*Valvata piscinalis, Viviparus viviparus, Lithoglyphus naticoides, Unio pictorum, U. crassus, U. tumidus, Sphaerium rivicola, S. solidum, S. corneum, Pisidium amnicum, P. supinum, P. henslowanum, P. casertanum, Dreissena polymorpha* and *D. bugensis*). In this lower part of the reservoir, the quantity of mollusks and their biomass account for 2,820 specimens/m^2 and 780 g/m^2 respectively.

The annual dynamics of the bottom fauna of the lower part of Poljansky Bay is characterized by pelophilic biocoenoses. They are represented by olygochaetes, mollusks, corophiids, gammarids, caddisflies larvae, chironomids and by other insects. *Dreissena* is the most abundant (36,000 specimens/m^2); *Viviparus viviparus, Valvata piscinalis* and *Theodoxus fluviatilis* can also reach great numbers. We would like to stress the abundance and variety of forms of mollusks of the genera *Sphaerium* and *Pisidium*. On silted sands these genera are represented by *Sphaerium rivicola, S. solidum, S. corneum, S. subsolidium, Pisidium amnicum, P. supinum, P. henslowanum* and *P. casertanum*.

The bottom fauna of pelophilic biocoenoses of Vorskljansky Bay, the largest bay of the Dneprodzerzhinsk reservoir, has a similar composition. The bottom is formed by silted sand mixed with detritus. In addition to the abundant *Dreissena*, other species of mollusks are *Radix ovata, Planorbis planorbis, Coretus corneus, Theodoxus fluviatilis, Valvata piscinalis, Viviparus viviparus, Lithoglyphus naticoides, Unio pictorum, U. crassus, U. tumidus* and *Anodonta cygnea*.

Among the thickets of higher aquatic plants in Poljansky and Vorskljansky bays the perfoliate pondweeds have the most diverse mollusk fauna. This fauna is composed of more than 10 groups of invertebrates, including mollusks. The malacofauna is rather diverse here; its quantity is 500 specimens/kg of plants. It is represented by the young of *Dreissena polymorpha, D. bugensis, Radix auricularia, R. ovata, Coretus corneus, Armiger crista* var. *inermis, Ancylus fluviatilis, Acroloxus lacustris, Theodoxus fluviatilis, Valvata piscinalis, Viviparus viviparus, Lithoglyphus naticoides, Bithynia tentaculata* and *Physa fontinalis*. The malacofauna of fennel pondweeds and various leaved pondweeds is less diverse; young *Dreissena polymorpha, Coretus corneus* and *Viviparus viviparus* account for 10 specimens/kg of vegetative substratum.

The fauna of milfoil differs by its high quantity of young *Dreissena*, especially *D. polymorpha* – up to 5,000 specimens/kg. *Viviparus viviparus, Bithynia tentaculata, Theodoxus fluviatilis, Dreissena polymorpha* and *D. bugensis* were also recorded from the fauna of the common reed, bulrush, sea scirpus and lesser reedmace.

Monodacna colorata, which is widely distributed in Samara Bay of the Zaporozhje reservoir, can be used for studies on acclimatization and the introduction of highly productive invertebrate animals for enriching food reserves of fishes of Poljansky and Vorskljansky bays.

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CHARACTERISTICS OF THE FRESHWATER MALACOFAUNA OF THE CRIMEA

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Abstract

Data on freshwater fauna of the Crimea are rather scanty, although such data are of considerable interest to studies of the effect of insular isolation upon the formation of the fauna, and for other aspects as well.

The spring collections of 1973 and the summer collections of 1974 served as a basis for the work presented below. Over 130 samples were taken in 4 zones of the Crimea: in the foothill and mountain forest zones, in East Crimea and on the south coast of the Crimea.

Data from the literature and our own observations show that the freshwater malacofauna of the Crimea is qualitatively poor. It is represented by 27 species, 13 of which (*Lymnaea auricularia, L. truncatula, Planorbis planorbis, Gyraulus albus, Physa acuta, Viviparus contectus, Unio stewenianus, Anodonta piscinalis, Dreissena polymorpha, Musculium lacustre, Euglesa casertana, E. pusilla* and *E. henslowana*) were found in the ranges of the investigated territory, and *Physa acuta*, which is reported for the first time in the Crimea. *Lymnaea truncatula* and *P. acuta* are most abundant in waterbodies of the south coast, East Crimea and the foothill zone, with *L. truncatula* occurring in 63.2%, 37.5% and 55.5% respectively of the populations. The above species (especially *L. truncatula*, an amphibiont species) differ in a broad ecological valency and, due to this, are found in waterbodies of different types — in quick-running mountain rivers, stagnant decorative ponds in parks and small stagnant waterbodies of the astatic type.

Among the lamellibranchiate mollusks, *Euglesa casertana* was the most widely distributed in the Crimea. This eurybiontic species prevails in the foothill and mountain forest zones, and on the south coast (their occurrence in the collections from these places being 31.5%, 30.8% and 20.6%, respectively). In the foothill zone, *Planorbis planorbis* (in 26.3% of the collections) and *Lymnaea auricularia* (in 15.9% of the collections) are quite common, and in the East Crimea, *P. planorbis, Gyraulus albus* and *Dreissena polymorpha* (12.5% occurrence for each species) are common. The latter species has recently migrated into Crimean waterbodies from the Kakhovsk reservoir after the opening of the North-Crimean Canal. In 1973, this mollusk was already found in the Theodossia reservoir. In the future, due to its planktonic larvae, a spread of *D. polymorpha* can be expected along the route of the canal from Vladislavovka to Kerch, where a number of water reservoirs are being created.

The finding of *Viviparus contectus* in an artificial waterbody near Frunzensky is very interesting. Up until now this species had been recorded only from the Tchernaja River drainage (near Sevastopol). It is not clear how it was introduced into this particular waterbody on the south coast of the Crimea.

The Crimea (where most waterbodies are ephemerical and cease to exist by the middle of April to the end of May) is characterized by great fluctuations in the density of mollusks from spring to summer. With a decrease in the area of the permanent waterbodies, caused by evaporation, the density of colonies of mollusks increases and can be rather high (e. g., *Lymnaea truncatula* with 8,400 specimens/m^2 and a biomass of 453.6 g/m^2).

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MOLLUSKS OF LAKE PSKOVSKO-CHUDSKOJE

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Abstract

Hydrobiologists of the Institute of Zoology and Botany have regularly collected zoobenthos on Lake Pskovsko-Chudskoje (Peipsi-Pihkva) from 1964 until 1973. The samples were taken from 22 sampling spots, every year at the beginning of June, and were taken from 50 shallow-water profiles around the whole lake in July and August, 1970.

Sixty-one species of mollusks (26 gastropods and 35 bivalves) were found in the lake; they are listed below.

Gastropoda: *Theodoxus fluviatilis* (Linnaeus), *Valvata cristata* Müller, *V. pulchella* Studer, *V. depressa* Pfeiffer, *V. ambigua* Westerlund, **V. antiqua* (Sowerby), *V. klinensis* Millet, **V. piscinalis* (Müller), *Viviparus contectus* (Millet), *V. viviparus* (Linnaeus), **Bithynia tentaculata* (Linnaeus), *B. leachi* (Sheppard), *Oxyloma pfeifferi* (Rossmaessler), *Lymnaea truncatula* (Müller), *L. stagnalis* (Linnaeus), *L. fusca* (Pfeiffer), *L. palustris* (Müller), *L. ovata* (Draparnaud), *L. ovata* form *patula* (DaCosta), *Planorbis planorbis* (Linnaeus), *Armiger crista* (Linnaeus), *Anisus vortex* (Linnaeus), *A. vorticulus* (Troschel), *A. albus* (Müller), *Segmentina nitida* (Müller), *Planorbarius corneus* (Linnaeus).

Bivalvia: *Unio tumidus* Philippi, *U. pictorum* (Linnaeus), *Pseudanodonta anatina* (Linnaeus), *Anodonta cygnea* (Linnaeus), *Musculium ryckholti* (Normand), *Amesoda scaldiana* (Normand), *Sphaerium corneum* (Linnaeus), **Pisidium amnicum* (Müller), **P. inflatum* Megerle, **Euglesa nitida* (Jenner), *E. fedderseni* (Westerlund), *E. crassa* (Stelfox), *E. pulchella* (Jenyns), *E. humerosa* Pirogov & Starobogatov, *E. tanuga* Timm, *E. ruut* Timm, **E. henslowana* (Sheppard), **E. dupuiana* (Normand), **E. suecica* (Clessin), *E. volgensis* Pirogov & Starobogatov, *E. tenuisculpta* Pirogov & Starobogatov, *E. difficilis* Pirogov & Starobogatov, *E. peipsi* Timm, *E. ponderosa* (Stelfox), *E. supina* (Schmidt), *E. conica* (Baudon), *E. globularis* (Clessin), *E. acuminata* (Clessin), *E. fossarina* (Clessin), *E. rivularis* (Clessin), *E. pihkva* Timm, *Neopisidium torquatum* (Stelfox), *N. alpinum* (Odhner), *N. stelfoxi* Pirogov & Starobogatov, **Dreissena polymorpha* (Pallas).

Large clams (*Unio, Anodonta, Pseudanodonta* and *Dreissena*) were excluded from the average number and biomass of the mollusks (because they were found very irregularly) and were dealt with separately. The number of specimens and the biomass of the big clams were rather high: 117 specimens/m^2 and 111.35 g/m^2 (the overwhelming majority formed by *Dreissena*).

The number and biomass of gastropods and small clams were comparatively low – 128 specimens/m^2 and 1.74 g/m^2. The mollusks dominated in number (271 specimens/m^2) in 1967 and in biomass (3.16 g/m^2) in 1972 (the high biomass in 1966 and 1972 was due to some large *Viviparus*). The number of mollusks was low (69 specimens/m^2) in 1972 and the biomass (0.73 g/m^2) was low in 1964.

The Pisidiidae formed 4.8% of the average number of specimens and 8.9% of the biomass of the total benthos (excluding the large clams), while the corresponding figures for the Gastropoda were 0.4% and 6.7%.

In the littoral zone (4 sample spots), small mollusks formed 1.0% (in 1972) to 8.6% (in 1968) of the average number of specimens in the whole zoobenthos, and 8.5% (in 1964) to 68.8% (in 1972) of the biomass. In the sublittoral zone (9 sample spots), the corresponding figures were 2.9% (1965, 1968) to 10.6% (1967) and 8.3% (1972) to 82.7% (1966). In the profundal zone (9 sample spots), the corresponding figures were 3.1% (1972) to 8.3% (1967) and 3.3% (1972) to 14.2% (1971).

*common in the whole lake

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A STUDY OF THE SPHAERIIDAE FROM THE UKRAINIAN PART OF THE CARPATHIAN MOUNTAINS

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Abstract

Mollusks of the family Sphaeriidae were collected from different Carpathian waterbodies during the period 1968-70. Natural waterbodies – mountain rivers, creeks, springs, natural and artificial lakes, ponds and water-supply canals of trout farms – were studied. Twelve species of sphaeriids were recorded. In the foothills and mountainous parts, the only species represented is *Euglesa casertana*, which occurs in dammed portions of rivers. In the Carpathians, this is a widely distributed species, occurring in different types of waters. It was recorded at a height of 1,745 m above sea level at a density of 7,000 specimens/m^2. *Euglesa casertana* is a component of biocenoses of artificial waterbodies in trout farms. It produces numerous populations in the mud or in the marginal aquatic vegetation, its density amounting

to hundreds and thousands of individuals per 1 m^2. *Euglesa obtusalis* was also recorded at a height of 1,745 m, especially on peat grounds.

Neopisidium conventus, Musculium terverianum and *Euglesa personata* are typical inhabitants of mountain waterbodies. The first species was found in the shore zone of Lake Sinevir (987 m above sea level). In small boggy areas, its density was up to 20 specimens/m^2. The discovery of *N. conventus* in Lake Sinevir is of considerable interest since it is the first report of this species from the Ukrain. According to data from the literature, this species is distributed in alpine lakes. Glacial Lake Sinevir is similar in its hydrobiological regime to high mountain lakes of the Alps and Caucasus. It is noteworthy that in waterbodies situated at different heights above the sea level, *N. conventus* inhabits only shallow areas. This regularity is confirmed by our material also. *Euglesa casertana* and *E. milium* were also found in the shore zone of Lake Sinevir.

Habitats of *Euglesa personata* are confined to shallow waterbodies of the mountainous part of the Carpathians. This species lives in cold waters at a height of 1,350 m above sea level. It is very abundant in springs with hard clay bottoms, a very rare phenomenon for sphaeriids. *Euglesa casertana* was also recorded from these waters.

Musculium terverianum was recorded only from waters of trout farms. The density of the colony was rather high, especially in areas with thickets of filamentous algae.

Stagnant waterbodies and natural ponds in the foothills are inhabited, in general, by *Musculium lacustre, Euglesa subtruncata* and *E. henslowana*.

Carpathian sphaeriids are represented, as a rule, by small ecoforms. The highest density of these mollusks was observed in oligotrophic waters.

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DISTRIBUTION, BIOLOGY AND ECOLOGY OF *SEMISULCOSPIRA CANCELLATA* IN THE UPPER AMUR DRAINAGE

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Abstract

From 1970 to 1974 a field investigation of the Amur and Lower Zeja (with its tributaries) was conducted in order to ascertain the biology and distribution of *Semisulcospira cancellata* (Benson 1833) in the Upper Amur drainage.

Semisulcospira cancellata was found in all investigated parts of the Amur and Zeja rivers, but its distribution was rather spotty in character. This species was completely absent from lakes; it is a mollusk which is adapted to running portions of streams, and in the Amur region it occurred in rivers and cut-off lakes. The majority of individuals were concentrated in the coastal area at a depth not exceeding 1 m.

In the southern Amur region, *Semisulcospira cancellata* occurred at the end of April or the beginning of May. All mollusks collected from the Burunda River on April 25, 1972 were inactive and their quantity in the coastal zone increased only by May 9.

Egg-laying in *Semisulcospira cancellata* begins at the end of the first week of May with its peak at the end of May or early June. The snails place their clutches on the shells of individuals of their own species or on the shells of other species and on other hard underwater objects (e.g., empty shells of bivalves, stones, etc.). However, the greatest number of clutches was found on individuals of the same species. Each clutch consists, on the average, of 233 eggs, with fluctuations in the number of eggs varying from 36 to 886 (56 shells with clutches were examined, 10 May). It was established that the number of eggs in the clutches depends on the size of the female laying them: in mollusks up to 2 g in weight the average number of eggs in a clutch was 240, from 2 to 4 g in weight the average was 276, and from 4 to 6 g it was 356. According to observations conducted on 9 May 1972, about 30% of the snails had clutches; by the beginning of June their number increased to 50%. In the 2nd half of July, the egg-laying intensity decreased considerably: 27 July, 6.6%; 28 July, 2.3%; 29 July, 2.2%; 30 July, 3.8%.

Young mollusks appeared at the end of July; these at first remained on the shell on which they were laid, which provided them with the best conditions for feeding and respiration.

At the end of July, a certain decrease in the number of mollusks was observed in the coastal zone, but the snails' true migration to hibernation sites south of the Amur region took place in October. Thus, in the Burunda River on October 18, 1972, only single individuals of *Semisulcospira cancellata* were found.

and by October 25 they were completely absent. At that time they could be found only at a rather great depth in groups of 5 to 10 individuals. In the upper parts of the Amur and Zeja rivers, the activity period of *S. cancellata* is 10 to 20 days shorter than in the region south of the rivers. Winter observations (during March 19-21, 1972) have shown that *S. cancellata* cannot stand great cooling; they die in frozen ground and survive only in those parts which do not freeze to the bottom.

Proceeding from the data obtained on the seasonal activity of *Semisulcospira*, a conclusion can be drawn that their infection with larvae of *Metagonimus yokogawai* takes place in the Upper Amur from the end of April or the beginning of May to the middle of October.

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ON THE BIOCHEMICAL AND MORPHOLOGICAL DIVERSITY OF *UNIO CRASSUS* PHILIPSSON

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Abstract

The question of conspecificity of the species *Unio crassus* Philippi is still disputable. On one hand, there are descriptions in the literature of a number of forms belonging to the *crassus* group which have the status of distinct species; on the other hand, there is the opinion that *U. crassus* from Europe is a widespread, but very variable species, which includes many forms that have been recognized as species.

Muscle myogens of 629 specimens of *Unio crassus* collected from the Moscow region were investigated using polyacrylamide gel electrophoresis. At the same time a morphological analysis of the same specimens was conducted (size characteristics of shells, the structure of hinge dentition, and the color of the foot and body).

An analysis of the electropherograms established the existence of 10 muscle myogen variants, which differ in the intensity of most mobile fractions. These differences were not associated with the sex, size or physiological state of the mollusks. A comparison of myogen spectra between allied species of the family Unionidae (*Unio pictorum* and *U. tumidus*, *Anodonta cygnea* and *A. piscinalis*) showed considerable differences in the position of the various fractions. In any given case, discrete differences were observed in the intensity of fractions, but there was complete coincidence in their positions on all the electropherograms.

A comparison of shells united into groups according to the variants of myogens showed that these groups can differ statistically in mean values of some characters, but that these differences are negligible and the shells cannot be arranged according to their morphological characters into groups corresponding to the types of myogens since the limits of characters coincide nearly completely. Differences between groups can be seen in various samples, but in different ways. Groups definitely differing in some character within one sample do not differ in other ones, or else they differ in quite other characters. No correlation was found between muscle protein variants and color of body and foot.

Having no grounds to regard each group of mollusks corresponding to a definite type of the system of myogens as a distinct species, we have tried to present a variety of these types as a display of intraspecie genetic polymorphism of muscle water-soluble proteins, basing our arguments on the presence or absence of intensive fractions in a rapidly migrating part of the spectrum. A check of the suggested model of phenotypic allelic determination showed that the phenotypic distribution corresponds to the Hardy-Weinberg law.

Thus, all specimens of the "*crassus*" group examined from different rivers of the Moscow region – which according to some authors can be different species – are, apparently, one very variable species, *U. crassus*. Since the spectrum of myogens of this species differs considerably from those of *U. pictorum* and *U. tumidus* (in all parts of the spectrum), then *U. crassus* should be separated as a distinct genus.

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PECULIARITIES OF THE PROTEIN COMPOSITION OF THE MYOGENES OF SOME LYMNAEID SNAILS

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Abstract

In order to establish the ranges of applicability of biochemical criterion in the taxonomy of lymnaeids, a comparative study of muscle myogens of various species was carried out by polyacrylamide gel disc electrophoresis. For this purpose, 6 to 10 individuals were taken of (1) *Lymnaea stagnalis* Linnaeus (Ls) from Lake Rytoe in the Smolensk region; (2) *L. danubialis* (Schrank) (Ld) from a waterbody near the town of Grjazi, Lipetsk region; (3) *L. berlani* Bourguignat (Lb) from the shores of Bukhtovy island, the Volga delta; (4) *L. atra* Schrank (= *L. corviformis* Bourguignat) (La) from Lake Rytoe, Smolensk region; and (5) *L. lagotis* (Schrank) (Ll) from 3 areas – the Volga delta, Kirov canal; the Tsarev River, Astrakhan; and the Volga delta, Kirov canal. (In the original Russian text, *L. danubialis* (Ld) and *L. berlani* have been cited erroneously as *L. palustris* and *L. taurica* respectively.) From the foot of each individual preserved in liquid nitrogen, a homogenate was made in tris-glycine buffer solution (pH 8.3). The ratio between the volume of buffer and the weight of the material was 1:10. The homogenate was maintained for 30-40 minutes in cold and then centrifugated for 20 minutes at 6,000 rpm. Only the supernatant was used for the electrophoretic investigations. The analyses were carried out according to Ornstein and Davis with equipment produced by the Hungarian firm "Reanal." For analysis, 7.5% separating gel and tris-glycine buffer pH 8.3 at 3-3.5 MA per tube was used; the duration of electrophoresis was 2.5-3 hours. The extraction of the gel columns was conducted in ice water, fixed with a 7% solution of trichloracetic acid, and stained in 0.05% amino black solution in 7% acetic acid for 12-18 hours. The gel columns were washed with 7% acetic acid. A great number of protein bands were separated: the bands were arranged into 7 main zones: pre-albumins, albumins, 1-globulins, 2-globulins, β1-globulins, β2-globulins and γ-globulins. (These fractions (up to 7) are usually separated by electrophoresis on paper.)

Our investigations showed well-reproducible protein zones in the gels for each species, with relatively constant individual electropherograms. A normal serum of man was taken as a standard. A comparative analysis of the electropherograms (Table 1) shows that the greatest differences are in the 2-globulin fractions, and, also, there are some specific peculiarities in the fractional protein composition of each species.

TABLE 1. Comparison of electropherograms of myogens of some lymnaeids.

Albumin fraction	Ld	Lb	La	Ls	Ll-1	Ll-2	Ll-3
Pre-albumins	1	2	1	1	1	1	1
Albumins	1	1	1	1	2	2	2
1-globulins	5	5	5	4	3	5	3
2-globulins	10	11	7	10	9	8	9
β1-globulins	1	1	1	1	2	1	2
β2-globulins	1	3	1	1	1	1	1
γ-globulins	2	1	1	1	1	1	1
Total no. of zones	21	24	17	19	19	19	19

For example, *Lymnaea berlani* is characterized by a greater number of pre-albumins; L_2- and especially β2-globulins are composed of subfractions. *Lymnaea danubialis* is characterized by a higher content of β2-globulins and a higher content of γ-globulin subfractions. It should be noted that despite some differences in subfractions for *L. lagotis*, the total number of subfractions for the 3 ecological forms was the same, which apparently reflects the specificity of tissue proteins in their genetic community.

Results of our investigations agree with data of other authors who have indicated species specificity of proteins and the usefulness of protein spectra in taxonomy (Logvinenko & Kodolova, 1971; Klimenko & Sazanov, 1972; Mancuso, 1964; Davis, 1967); our study further emphasizes the advantages of this method in taxonomy).

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THE ENERGETIC BALANCE IN POPULATIONS OF BIVALVES

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Abstract

Energetic principle of research of ecological systems holds a special place in recent ecology. Its use requires a study of the energetic balance of growing individuals and populations.

In *Unio tumidus*, *Sphaerium suecicum*, *Pisidium crassum* and *P. lilljeborgi*, changes were considered taking place in the consumed and assimilated energy during the growth of each individual. The changes manifest themselves in the regular decrease of the plastic metabolism share during the development of the individual. The coefficient of assimilated food energy utilization for growth (K_2) at early developmental stages of mollusks is close to 70-80% and at the end of life does not exceed 10-15%. An average value of K_2 is also of great ecological importance for a growing animal.

A study of the correlation between energetic and plastic metabolism in populations of different species has shown that the mean value of K_2 for the mollusk population for a growing season (or year) and K_2 of the growing individual of the same species are close to each other. This points to the prevalence of middle-aged individuals in populations. The energy flow (A) (assimilated energy) through a population is a function of its average biomass (B) and can be approximated by the equation $A = \gamma B^{\alpha}$, where γ and α are parameters of the equation and the value α does not differ confidently from unity. As far as $A = P + R$, where P is population production, R = expenditures for metabolism and $K_2 = P/A$, then the population production can be determined as $P = \gamma \cdot B \cdot K_2$. Parameter γ is the intensity of the energy flow through a population when its biomass is equal to unity. Thus, the population production is determined by an average biomass value for season (year), intensity of the energy flow and by the value of K_2 for the same period. So, the production of a population is a result of static, dynamic and functional aspects of the populations studies.

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THE FILTRATION ABILITY OF *DREISSENA BUGENSIS* ANDRUSOV

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Abstract

Animals were caught in a waterbody before the experiment and were kept for 2 days in a suspension of *Chlorella* sp., the concentration of which was up to 0.1 mln cells per ml. The animals were then placed into glasses (250 ml volume) filled with water from the same waterbody and with a pre-set concentration of Protococcaceae which varied from 0.081 to 0.980 mln cells/ml (the difference between the minimum and maximum value was more than 12 times). The average diameter of the cells was 4 μ. Two to 5 specimens of small mollusks (5-10 mm) were placed in 50 ml of algal suspension, while 1 specimen of a larger size (10-31 mm) was placed in 100 ml of suspension. Simultaneously, a control test was made. The experiments lasted 1-2 hours at a temperature of 20.3°C, and they were repeated from 3 to 11 times. Variations in the concentration of algae were determined by the change in the optical density of the algal suspension on a photoelectrocalorimeter. Results were compared with those obtained by a direct count of *Chlorella* sp. under the microscope.

The filtration rate (the water volume filtrated by mollusk per unit time) was estimated by the formula $v = m \left(\frac{\ln Co - \ln Ct}{t} - a \right)$, where v = filtration rate, ml/hr; m = volume of experimental suspension in ml; t = duration of experiment in hours; a = correction of the non-biological sedimentation of algae; and Co and Ct = the initial and final concentrations of algal suspension.

The results of these investigations were treated statistically. The difference values were estimated at the 95% confidential level. The significant differences were estimated (t) according to Bailey (1959). The difference was considered as significant at $t/t\ 0.05 > 1$, where t = estimated and t 0.05 = the critical

table value of criterion t. When having a significant difference, we could express sample difference ($\triangle X$) in % to the initial value.

It was established that in mollusks of different size the filtration rate depends on the size (weight) of the animals. A tendency was observed to increase the absolute filtration rate (X_1) with increasing size (weight), while the relative filtration rate (X_2, per 1 g of living weight) decreases with increasing size of the mollusks.

Thus the filtration rate of individuals from 5 to 10 mm (0.0608-0.3968 g) at the concentration of algae of 0.240 mln cells/ml was 2.31 ml/specimen/hr. With an increase in size of the animals to 26-31 mm and weight to 1.5346-3.6940 g, considerable differences were observed in the filtration rate of mollusks, and the relative value of the sample difference can reach 95.9%. The same dependence takes place during measurement of the values studied at different concentrations of algae. For example, the volume of water filtrated by a mollusk 11-15 mm in size for 1 hour at a concentration of 0.980 mln/cells/ml was 7.57 ml/specimen/hr.; for a specimen 16-20 mm, it was 8.39; for a specimen 21-25 mm, 9.78; and for 26-31 mm, 11.33 ml/specimen/hr.; relative values of the filtration rate are correspondingly equal to 13.25-9.16-5.46-4.21 ml/specimen/hr. The filtration rate at the concentration of suspension 0.980 mln/cells/ml between individuals of size groups 11-15 mm and 16-20 mm was significant and its value can reach 51.2%; between animals 11-15 mm and 21-25 mm in size the relative value of the sample difference was 49.4%; for animals 16-20 mm and 21-25 mm, it was 49.1%.

With the increase in the concentration of algae from 0.081 mln to 0.980 mln cells/ml the water filtration rate in the size group 16-20 mm decreased by 76.9%, in mollusks 21-25 mm in size it decreased by 81.7%. Comparing the obtained values with filtration rate values known for *Dreissena polymorpha*, we see that our data are close to those obtained by Voskresensky (1957), Kondratjev (1969), and others. Thus, *D. polymorpha* at a temperature of 15.6-18.2°C can filtrate 2114 cm^3 in 24 hours (its average size 298 cm^3), and at 17-18°C a mollusk 20 to 30 cm in length can filtrate 1.5-2.0 l of water in 24 hours.

Empirical data obtained for *Dreissena bugensis* shows that these animals, depending on their size (weight) and concentration of Protococcaceae, can filtrate to 1375 cm^3 of water. According to Mikheev (1965), the relative filtration rate of *D. polymorpha* is 20-25 ml/g/hr.; according to Kondratjev (1962), this value varies from 11.0 to 74.0 ml/g/hr. The relative filtration rate of *D. bugensis* varied from 4.21 to 57.80 ml/g/hr.

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MECHANISMS OF ADAPTATION OF TISSUES OF *ANODONTA CYGNEA* LINNAEUS TO VARIOUS CONCENTRATIONS OF CALCIUM IN WATER

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Studies were undertaken of tissue reactions of hepatopancreas, mantle, muscles and glandular apparatus of gills of *Anodonta cygnea* Linnaeus to short and long effects of various concentrations of calcium (0.5-4.0%) in water. Biochemical and histochemical characteristics of the distribution of calcium in tissue structures were given; peculiarities of tissue respiration, of energetics and water – salt metabolism in mollusks during their adaptation to higher calcium concentrations in water – were defined. In particular, a high intensity of calcium metabolism in the mantle, and especially in its glandular formations near the shell, has been shown. It was found that calcium accumulation in tissue and cell structures of the above glandular organs causes changes in the content of general and nonorganic phosphates, natrium, potassium and water.

Adaptation of mollusks to high calcium concentrations in water is accompanied by the increase in energetic expenditures of the organism. This was proved by tissue changes in the ATP-activity and in activity of respiratory enzymes. It should be noted that tissue consumption of oxygen varied in different ways depending on the calcium concentration in water and duration of the experiment. Thus, during the first 24 hours of the experiment (in water containing 0.5-1.0 °/oo of calcium), tissue consumption of oxygen determined by the polarographic method was higher in mantle and muscles. At the same time, the activity of succinate dehydrogenase and cytochrome oxydase in tissue preparations of hepatopancreas, gills, mantle and muscles sharply increased. By the end of the 7th day, the respiration intensity of tissues, the activity of respiratory enzymes, the general and nonorganic phosphorus content and the

general water were close to primary values.

At higher (2.4-4.0 °/oo) calcium concentrations in water, the tissue oxygen consumption did not increase, although the activity of respiratory enzymes remained higher. This suggests the possibility of a transition to anaerobic metabolism under conditions of extremely high calcium input.

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THE ROLE OF PULMONATE SNAILS IN THE SHALLOW WATERS OF THE DNIEPR RESERVOIRS

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The development of the pulmonate snail fauna in the Dniepr reservoirs is affected by such factors as water exchange and the snail's position in the water flow. In the upper water reservoirs and in reservoirs with intensive water exchange, 14-15 species are common in shallow waters; in reservoirs occupying an intracascade position, due to the lack of side inflow, the number of these mollusks is limited to the 5-6 most common species of the group.

The distribution and the level of quantitative development of pulmonate snails depend on the morphometric and hydrological characters of water reservoirs and on the nature of initial territories. Their greatest aggregations and specific variety are confined to poorly flowing waters of the floodplain and secondary terrace. The role of pulmonate snails in the benthos is especially significant at small depths limited to the isobath of 1 m, where they account for 70-90% of the total biomass of phytophilous invertebrates. The role of phytophilous Pulmonata in the total productivity of mollusks in shallow waters can vary from negligible to one of paramount importance. In the first years of the existence of the Kiev water reservoir the production of pulmonate snails was, on the average, about 40% of the total production of mollusks.

The age of the water reservoir determines, to a considerable extent, the part played by pulmonate snails in the productivity of coastal invertebrate communitites. A mass outbreak of productivity of these animals in the first years of a reservoir's existence is meaningless in that it is limited in space and time, which are much more important for homotopic animals.

Such outbreaks take place, as a rule, only in the parts of the floodplain in upper portions of water reservoirs; a sharp increase of the level which usually occurs in succeeding years of their existence results virtually in the death of the mollusks. This process is especially pronounced in relatively deep-water reservoirs, e.g., the Kremenchug reservoir.

Restoration and further increase in the number of coastal phytophilous pulmonate snails proceed rather slowly as compared to waterbodies of the river system that are associated, to a considerable extent, with great changes in their level. This process is especially protracted in intracascade reservoirs without significant tributaries (e.g., the Kakhovka reservoir).

The role of pulmonate mollusks becomes more important in the productivity of shallow waters in reservoirs existing over 5 years. In the Kiev water reservoir, in 3 years after its filling, the stock of *Lymnaea stagnalis* amounted to 630 tons and in 7 years to 1779 tons. In the Zaporozhje water reservoir, in 22-23 years the biomass of *Coretus corneus* amounted locally to 150 g/m^2, and the biomass of *L. stagnalis* and *Radix ovata* amounted to 60 g/m^2. In the river floodplain such biomasses can be expected only during the flood period, when mollusks are aggregated in the coastal zone.

Pulmonate mollusks play an important part in the turnover of organic matter as far as they are mass consumers of higher aquatic vegetation and filamentous algae. The consumption of plants by other phytophages, due to their low quantity, comes to .1 and .01% of their production. In the Kiev water reservoir 2 populations of *Lymnaea stagnalis* and *Radix ovata* can consume for a vegetation season about 6% of the filamentous algae production and about 5.5% of the production of the fennel pondweed. In Zaporozhje reservoir *L. stagnalis* consumes up to 16 g/24 hr. of filamentous algae and 9 g/24hr. of pondweeds. Under the same conditions, *R. ovata* consumes 6 g/24 hr. of filamentous algae and 3.7 g/24 hr. of pondweeds.

Many species of the genera *Lymnaea, Radix, Coretus* and *Galba* are intermediate hosts of trematodes pathogenic for fishes and man. The greatest specific variety of larvae and parthenites of trematodes and the infection intensity of intermediate hosts coincide with the mass development of pulmonate snails in the first years of the existence of water reservoirs. An impoverishment of the trematode fauna takes place in 2-3 years against a background of quantitative depression of the Pulmonata. Stabilization of the specific composition and quantity of pulmonate snails favors an increase in their infection.

The highest infection rate of mollusks is observed in shallow waters of the upper parts of reservoirs and in bays of side tributaries that are associated with a concentration of definitive hosts (water fowl and young fishes) and with a flow of larvae along tributaries.

The development of trematodes, larvae of which parasitize pulmonate mollusks, is characterized by nidality. In the Kiev reservoir there are nidi of parasitic infections (*Tetracotyle, Diplostomum*) dangerous for young fishes. In the Kremenchug reservoir, an intensive development of trematodes of the families Sanguinicolidae and Diplostomatidae was recorded. Sanguinicolosis is especially dangerous for the young game fishes. The main intermediate hosts of these pathogenic species are lymnaeids, generally *Radix ovata.*

The intensity of parasitism in shallow waters of the Dniepr reservoirs does not depend on the quantity of intermediate hosts. Very often there is a reverse dependence between quantity of Pulmonata and intensity of infection: populations with smaller densities were found to have higher infections. If their quantity is high, pulmonate snails play a very important part as degraders of detritus in the general balance of organic matter, thereby participating in the natural purification processes. The negative role of mollusks in the circulation of pathogenic species of parasitic trematodes can be much reduced by complex measures of control of dangerous parasite nidi.

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THE ROLE OF *VIVIPARUS* IN THE DESTRUCTION OF ORGANIC MATTER IN THE MIDDLE DNIEPR

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Abstract

Viviparus viviparus populations from the Middle Dniepr (Tripolje region) were studied. The growth rate, metabolism intensity, fecundity and quantitative development of mollusks were investigated.

The size-weight indices of *Viviparus* are characterized by the following values: the dependence between the length (l) and weight (W) of the body is expressed (on the basis of 540 measurements) by the equation:

$$W = 0.307\, l^{(3.21 \pm 0.0,3)}$$

with a high correlation coefficient, 0.998. The ratio between raw and dry weight (W_1) of the body is represented by the equality $W = 8.3\ W_1$. The shell weight amounts to, on the average, 40% of the total mollusk weight.

The growth rate determination was conducted at 2 temperatures (18±1° and 24±1°C) corresponding to those temperatures when the material was collected (spring and summer temperatures). Curves of the mollusks' growth under laboratory conditions estimated for 2 temperature intervals point to the increase in the growth rate with an increasing temperature that is in agreement with empirical data. The equations obtained are as follows:

at 18±1° $Wt = (1.565 - 1.276e^{-0.03t})\ 4$
at 24±1° $Wt = (1.565 - 1.276e^{-0.0043t})\ 4$

where Wt = values of the absolute increment, t = growth duration in days, e = base of natural logarithms.

From the sections of the empirical growth rate curve that were obtained and the estimated theoretical curve, an average daily absolute increment was determined for an individual of average weight 1.9 g, which accounts for 20 mg/day. On calculating the theoretical growth curve, K_2 (the coefficient of the use of energy of assimilated food for growth) at each temperature was assumed to be equal to 0.3.

Experiments on the determination of *Viviparus* metabolism intensity were conducted from May to August, the interval in weights of experimental animals was from 0.02 to 6.00 g. Within the ranges of a water temperature from 18.6 to 30°C, the metabolism intensity increased about 2 times, the coefficient A in the equation of the dependence of metabolism on body weight ($R - AW^k$) changed from 0.075 to 0.190 (calculated for the whole organism) and from 0.125 to 0.265 (calculated for soft parts of the body). The exponent – coefficient k – in 6 obtained equations was from 0.76 to 0.83. The general equation reflecting the quantitative side of the interrelation between the metabolism and weight of *Viviparus* is expressed by the following parameters:

$$R = 0.105\ W^{(0.77 \pm 0.026)}$$

The correlation coefficient between lgR and lgW was rather high – 0.99.

Seasonal differences in the respiration intensity of mollusks and other invertebrates are also found in *Viviparus*. Thus, in spring and by the end of the summer, all *Viviparus* have the same metabolism intensity despite the differences in a temperature regime. When autumn comes the metabolism intensity decreases.

In the region investigated, the average quantity of *Viviparus* was 265 specimens and the biomass was 500 g/m^2. Reproduction took place the entire growing period (May-October). The average individual fecundity of females was 18 to 20 specimens.

Feeding by filtration and consumption of decayed vegetable and animal tissues, according to literature data, point to the possible important role of these animals in self-purification processes.

On the basis of obtained values and those known from the literature on growth rate, feeding and metabolism, we calculated, in the first approximation, energetic expenditures of a *Viviparus* population in the Dniepr. Assuming that 18°C is the average temperature for a growing period, we estimated that expenditures for metabolism in a population of mollusks per 1 m^2 for a growing period (220 days) amount to 1342 kcal. Incremental expenditures are 583 kcal, if the calorific value of *Viviparus* is assumed to be 0.5 kcal/g of the whole raw organism. Thus, assimilated food summed up by increment energy (P) and by energy for respiration (R) accounted for 1925 kcal. The ration value (C) was estimated in 2 ways: a) by using materials on feeding intensity of *Viviparus* (Tzikhon-Lukanina, 1965) after necessary calculations, and b) by assuming that assimilation is equal to 45%. We obtained a value of the same order of magnitude, – 4278 kcal. Hence, using a balanced equality, it is easy to calculate a nonassimilated portion of food (F)

$$F = C\text{-}P\text{-}R$$

F amounts to 2353 kcal. Consequently, 55% of assimilated food is excreted by mollusks, and apparently it forms a part of the ground waterbody.

Estimating the indices of the participation of *Viviparus* populations (density 265 specimens/m^2) in the destruction of organic matter, we can evaluate their functional role in the self-purification process in the Middle Dniepr. According to our calculations, a quantity of oxygen equivalent to the destruction of 1 g (5 kcal) of ashless organic matter is necessary for energy metabolism in *Viviparus*. If the organic suspension in water amounts to 17 kcal/m^3, *Viviparus* mineralizes 5 kcal/24 hrs/1m^2, which accounts for 29% of its organic matter.

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PHYSIOLOGICAL ASPECTS OF ADAPTATIONS OF MOLLUSKS TO ABIOTIC AND BIOTIC FACTORS DUE TO BLUE-GREEN ALGAE

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Abstract

The construction of water reservoirs on the Dniepr River has created prerequisites for water "florescences" caused by the development of blue-green algae. Our investigations on fish have shown that products of vital functions and decay of algae taken in a quantity of 0.6-5 g/l are lethal for fishes and cause specific metabolic disturbances, such as B_1-avitaminosis, which is intensified by a worsening of the gas regime. In this connection, a study of physiological adaptations of mollusks to the effects of blue-green algae (*Microcystis aeruginosa* Kütz emend. Elenk. was used in our studies) is of great interest. For our investigations, *Dreissena polymorpha*, *Dreissena bugensis* and *Galba* (= *Stagnicola*) *palustris* were chosen. Two species of *Dreissena* were studied because in all of the Dniepr water reservoirs *D. polymorpha* is replaced by *D. bugensis*, apparently due to blue-green algae.

We established the specificity of reciprocal reactions of mollusks to the effect of algae. Concentrations of *Microcystis* from 10 to 25 g/l were found to be lethal for *Dreissena*. Under such conditions, *Dreissena* did not open their shells and did not feed. The mortality of these mollusks was from 30 to 100%, and depended on the concentration of algae in the water and on the time of their influence. *Galba palustris* did not die even at 25 g/l concentration of algae, but specimens of this species were not mobile,

as if they were in a state of quiescence. However, they consumed algae. How to explain the survival of mollusks under the conditions which usually are lethal for fishes? Bivalves have little mobility and some of them, including *Dreissena*, are sessile forms. So when the environment lacks oxygen, the mollusks cannot avoid asphyxia. The existence of numerous generations under such conditions has led to the development of a number of adaptative mechanisms: mollusks decrease their energy requirements to a minimum, partially or completely change an aerobic type of metabolism to an anaerobic one. The latter is not effective from the point of view of energy outflow and it leads to an accumulation of incompletely oxidized metabolic products, but it enables the animals to survive hypoxia or anoxia.

During the processes of anoxidial splitting, carbonic acid is excreted as a final product without oxygen consumption. Therefore, the respiration coefficient in anoxibiotic animals is extremely high. For 2 days of the experiment in water, with *Dreissena* as controls, the oxygen content decreased by 35-54% as compared to the primary value; in water with 25 g/l of *Microcystis*, the oxygen content decreased by 65-84%. Especially significant was the oxygen fall in the water containing *D. polymorpha*. This was due to the oxygen consumption by mollusks and the expenditures of destruction processes of algae. Concurrently with the oxygen decrease, an increase was observed in the carbonic acid content. In water with *D. bugensis*, under the effect of *Microcystis*, the carbonic acid content increased about 5 times (28 mg/l), and in water with *D. polymorpha* it increased 6 times (43 mg/l) – as compared to controls (5 and 6.6 mg/l). The oxygen consumption was higher in *D. polymorpha* (0.97 mg/g/hr.) than in *D. bugensis* (0.88 mg/g/hr.). After 5 days exposure of *Microcystis* upon *Dreissena*, there was noted a decrease in the respiration intensity, especially in *D. polymorpha*, and a greater carbon dioxide excretion. The respiration coefficients were 3.55 and 16.77 in *D. bugensis* and *D. polymorpha* respectively.

It is known that mollusks are characterized by a considerable accumulation of carbohydrates. The intensification of glycolytic processes results in the rapid consumption of glycogene reserves in *Dreissena*; in dry weight, a definite decrease in carbohydrates was observed as compared to controls – by 72% in *D. bugensis* and by 83% in *D. polymorpha*. Lipids decreased by 27 and 11% respectively. In *Galba palustris*, which consumed *Microcystis*, the carbohydrate expenditures were less than in *Dreissena* (46%).

No changes were found in the protein content of mollusks, but the quantitative content of free amino acids varied, especially in *Dreissena polymorpha*. A definite increase was reported in *D. bugensis* in the total amount of lysine/hystidine, and a decrease in the total amount of methionine/valine. A definite increase in the quantity of cystine, arginine, glutamic acid/treonine, alanine, phenylalanine and leucine was observed in *D. polymorpha*, whose anaerobic metabolism was more complete and longer than that in *D. bugensis*. A 2-fold rise of free glutamic acid points to deep disturbances in the protein synthesis due to the inhibition of the preamination reaction. Threonine, alanine and glutamic acid are links of carbohydrate, fat and protein metabolism, and undergo changes. Cystine, as is known, participates in the oxidation reduction processes and its quantity rises at asphyxia. This apparently can be explained by the availability of the active group, the sulfhydrilic one in particular, which is of special importance in regard to effects of various toxic substances. Under the influence of blue-green algae, the content of sulfhydrilic groups increased by 73% (from 1.09 to 1.89 m/g) in *D. polymorpha* and by 59% (from 1.24 to 1.97 m/g) in *D. bugensis*.

Adaptation to anaerobic conditions is also accomplished in mollusks by the excretion of final metabolic products, the accumulation of which could result in intoxication of the organism. Urea, for example, is such a product. Arginine and transaminases, glutamic-alanine (ALT) and especially glutamic-asparagine (ACT), take part in the synthesis of urea. During the experiment, under the effect of blue-green algae, the activity of ACT increased by 91.67% (from 16 to 22.2 unit/mg in *Dreissena bugensis* and by 38.75% in *D. polymorpha)*. The activity of ALT increased, but to a lesser extent: by 42.8% (18.2 to 26 unit/mg) in *D. bugensis* and by 25.82% (27.6 to 34.6 units/mg) in *D. polymorpha*.

As noted above, the effect of algae on fishes results in an increase in thiaminase activity and a sharp fall in thiamine content. Quite another regularity was observed in mollusks: in *Dreissena* (especially in *D. polymorpha*) and in *Galba palustris*, the thiaminase activity fell by 17-28%, as compared to the control. At the same time the thiamine quantity increased by 28% in *G. palustris* and by 13% in *D. bugensis*, while in *D. polymorpha* it decreased by 57%. This apparently is explained by the adaptation of hydrobionts to detoxication of the toxic influence of intermediate products of anaerobic metabolism by excreting them into the environment, and for mollusks, into the liquid of mantle cavity as well. It is very possible that the decrease of thiaminase activity in the mollusk organism is associated with its excretion into the environment, which allows the mollusk to avoid hypovitaminosis.

Thus, the adaptation of mollusks to the effect of rather high concentrations of blue-green algae is accomplished by the mollusks' ability to exchange a partially or completely aerobic type of metabolism for an anaerobic one, and to detoxicate various toxic matters by their excretion into the environment. Gastropods resist the effect of algae better than bivalves due to this double type of respiration: oxygen dissolved in water and gas-like oxygen. *Dreissena polymorpha* is a more oxyphilous form than is *D. bugensis*. Under the influence of blue-green algae, it switches more completely over to anaerobic metabolism and makes better use of the homeostasis mechanism providing the permanence of the internal

medium and biochemical structures of the organism. A conclusion can be drawn that the substitution of *D. polymorpha* for *D. bugensis* in the Dniepr water reservoirs does not depend on blue-green algae.

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ON SOME REGULARITIES OF THE GROWTH AND PRODUCTION OF MARINE MOLLUSKS IN DIFFERENT TOPOGRAPHICAL/GEOGRAPHICAL ZONES

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Abstract

In spite of a vast literature on growth rates and life durations of mollusks, and in spite of a variety of methods by which we can define these important processes, all aspects of molluscan growth cannot be considered to be completely elucidated. In particular, the determination of the duration of life of individuals belonging to the same species under similar conditions but by different methods and by different authors very often differs by at least one order of magnitude.

For elucidating variability and general regularities of growth and productional processes associated with it, over 20 species of gastropods and bivalves from different topographical/geographical zones were investigated to analyze the structure of local populations and morphological characters of growth. The growth rate and general character of its decrease with age proved to be similar in species with similar size/weight indices independent to the geographic zone of their habitat or taxonomic status. Allied species most similar in shape and size possess the maximum similarity in their growth characteristics. Absolute growth rates in different taxonomic groups increase with increasing limiting sizes (weight) which can be reached by individuals of species populations.

It was found that the growth rate and life duration are minimum in small mollusks (*Minolia, Falsicingula, Hydrobia, Turtonia*, etc.; their life duration does not exceed 1-2 years), greater in mollusks of average sizes (*Littorina, Musculus*, etc.; life duration of 5-6 years) and maximum in large gastropods and bivalves (*Neptunea, Buccinum, Patinopecten, Crenomytilus*, etc.; life duration of 8-10-18-20 years).

The absence of a noticeable decrease in growth rates and an increase in life duration of arctic mollusks species as compared to boreal ones (this does not agree with a widespread opinion on the great deceleration of growth and maturation in species inhabiting cold waters) results from a genetic compensation which permits a rather high activity of enzymes at low temperatures. It should be noted that the effectiveness of the use of assimilated food in growth is noticeably greater in cold-water species than in warm-water species. This is associated with an increase in the relative share of bioenergy for growth, which apparently proceeds because low temperatures inhibit energetic expenditures for metabolism to a greater extent than those for growth (in arctic organisms, expenditures for metabolism are 3-4 times lower than in boreal organisms at summer temperatures). It is possible that lipids having a high caloric value play a more important part in the diet of cold-water forms than in that of warm-water forms. The most economic, direct (without pelagic larva) development prevailing in species inhabiting high latitudes is also of great importance for rapid growth at early ontogenetic stages.

As to the populations studied (over 70), their individuals at early stages of postlarval ontogenesis have exponentially limited growth periods, after which a gradual deceleration of growth takes place, approaching parabolic growth when the animals become mature. So, when plotting curves of linear growth or weight growth on a logarithmic scale, it is easy to define time (and size) when individuals of different species reach maturity under particular conditions. A parabolic character of growth in mollusks after reaching maturity is indicative of a regular deceleration in the growth rate and intensity of expenditures for metabolism at mature stages of ontogenesis. Disturbances of these relationships result in a disorder of the energetic balance of the organism, an increase in relative entropy in its metabolism and to natural death. The latter should be taken into account for the determination of the growth rate and age limit of mollusks by indirect, not ecophysiological, methods.

Individuals reach their maximum size and their maximum life duration under close to optimal conditions. Intraspecies group variability in growth rate, which depends mainly on temperature and other physical and chemical conditions in the geographic ranges of the species, does not exceed 20-30% in the species studied. Individual variability of growth rates is maximum in species with a protracted spawning

period, and it depends to a considerable extent on temperature conditions at early stages of postlarval ontogenesis. Due to an unequal effect of the same temperatures on the growth rates of organisms of different ages (at earlier stages of ontogenesis organisms are more sensitive), individuals appearing in populations at the beginning of the warm period have a greater growth rate and reach greater sizes in a year than those appearing at the end of the warm period and tolerating at the same phases of ontogenesis the effect of low temperatures.

It is clear that the production reflecting the growth and eliminations from the general population is a more significant factor in theory and practice than the growth of individuals, which cannot be confidentially defined without knowledge of peculiarities of individual growth. The productional process rate, which depends on the size/weight (age) structure of populations, is associated with thermopathy of species, and in different biogeographical groups it is maximum in different parts of the aquatoria at different times. Production and bioenergetic potential in allied species with similar size/weight characteristics are comparable in different topographical/geographical zones according to the origin and distribution of each species. In those parts of the aquatoria which differ in physical and chemical regimes, the productional process of the same species proceeds in different ways. Fluctuations in the production are maximum in species with short life cycles and in populations subjected to sharp changes in environmental factors.

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APPLICATION OF THE MAIN-COMPONENTS METHOD FOR THE ANALYSIS OF MORPHOMETRIC INDICES OF GROWTH AND FOR THE ESTABLISHMENT OF AGE IN MOLLUSKS

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Abstract

A study of bioenergetics of mass components of the ecosystem is closely connected with studies of general regularities of growth and definition of the age of an animal. The present paper considers the regularities of the growth of *Anodonta piscinalis, Unio tumidus* and *U. pictorum*. The main-components method was employed.

The size/age structure of the populations were investigated by means of 6 parameters: length (L), width (S), height (H), general weight (Wg), shell weight (Wsh) and body weight (Wb) of mollusks.

Having applied the above method we obtain instead of curves characterizing the growth of each parameter, several generalized characteristics, the 1st of which describes the most general regularity of the growth of the parameters, the 2nd describes the next common peculiarity of the growth which is not described by the 1st characteristics, and so on.

The value of a relative contribution of each morphometric parameter into this or that regularity can be easily established by means of the corresponding values of the main vectors. Our data have shown that the first two components describe 96-97% of the sum dispersion. This means that changes in the growth rate of all investigated parameters are subject virtually to 2 main regularities.

The parameters of all mollusks enter the 1st component with nearly equal contribution and identical sign. This shows that the proportional increase in size and weight parameters of the mollusks during their life is the main regularity of the growth.

The 2nd component is also formed by all parameters but the difference in the value of contribution is somewhat greater. The main character of the 2nd component should be noted – weight and size characteristics have opposite signs.

The availability of such reversely directed changes in the increase of size and weight of mollusks is the 2nd regularity of their growth overlapping the 1st main one.

With the age of mollusks the 1st component changes according to the linear law, i.e., takes place a proportional increment of all size and weight parameters of the mollusks.

Changes in the 2nd component show that the even growth of mollusks is complicated by different ratio between increments of size and weight parameters in different periods of life. Before reaching the sexual maturity linear sizes of mollusks increase somewhat quicker than weight ones; in a mature state the weight rise outruns the growth of linear sizes.

By the end of life the ratio between linear and weight parameters of mollusks returns to the initial one.

In nature takes place a common effect of 2 regularities of the growth. If each mollusk studied is represented in coordinates of two first components then it will be clear that they are arranged rather irregularly and form areas of concentrations and diffusions. Linear and weight characteristics of the centers of concentrations coincide with these of each age group defined before by annual rings. Hence, a conclusion can be drawn that the main-components method can be used for determination of a mollusks' age.

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STATISTICAL ESTIMATION OF THE COEFFICIENT OF BERTALANFFY'S GROWTH EQUATION FOR *CERASTODERMA LAMARCKI* AND *PARVICARDIUM EXIGUUM* IN THE AZOV SEA

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Abstract

Cardiids are now found in 42.2 to 71.8% of the area occupied by the Azov Sea, and form 98% of the total biomass of the zoobenthos. *Cerastoderma lamarcki* and *Parvicardium exiguum* play an important part in the feeding of benthophagous fishes. In this connection, the productivity of these mollusks is of great practical interest.

Seasonal observations on *Cerastoderma lamarcki* and *Parvicardium exiguum* were carried out in the Azov Sea for 2 decades. It has been found that the biomass of *C. lamarcki* varies in different years and seasons from 158 to 448 g/m^2 and that the biomass of *P. exiguum* varies from 30 to 50 g/m^2. The role of the latter increases with increased salinization of the sea. As to the food value of *P. exiguum*, it has a number of advantages over *C. lamarcki* due to its thinner shell and small size; it can be completely consumed by fishes, while only 50-60% of the *C. lamarcki* population can be used as food.

Average weights (general, body and shell) of the same size individuals vary in different years in wide ranges. In the period of 1954-59 these indices were the highest, which apparently is connected with favorable conditions of their habitats: a high dynamics of waters, ground compaction and no mass death through a low oxygen level of the water. In the period of 1960-66, when frequent mass death took place, the average weights of oxyphilous mollusks were considerably lower. A decrease in weight in this period was recorded from all size groups. Thus, the weight of *Cerastoderma lamarcki* individuals of the same size (up to 5 mm in length) was 35% lower.

In connection with the changing regime of the Azov Sea due to salinization and pollution, a necessity arose to trace the growth of dominating species in order to determine their present productivity. With this aim in view we conducted experiments on the study of the growth of mollusks in retainer cages (at Obitochnaja Key, Azov Sea).

In the experiment, metal frames covered with capron net N13 were used. Retainer cages were placed at a depth of 7-8 m. In each cage were placed, in 1 mm intervals, from 80 to 100 mollusks belonging to the same size group. At the beginning of the experiment the animals were measured with sliding callipers and weighed on a torsion balance. Measurements were repeated each 10, 20, 30 and 50 days. Thus, average daily linear increments $\triangle l/\triangle t$ (mm/days) of individuals of the same size were obtained. In all, 1049 specimens of *Cerastoderma lamarcki* and 655 specimens of *Parvicardium exiguum* were investigated. At the same time, for *P. exiguum*, the nitropaint tracer technique was used. Observations on some individuals enabled us to ascertain individual increments of traced specimens. Then an equation of the linear growth rate was obtained by means of the least square method:

$$\triangle l/\triangle t = a + bl \qquad (1)$$

Equations of the regression and their statistical characteristics are given in the table below.

Species of mollusk	n	$\triangle l/\triangle t = a + bl$	σ_b	σ_a	σ^2 res.	r	σ_r
C. lamarcki	50	$\triangle l/\triangle t =$	0.0007	0.439	0.0005	0.87	0.04
P. exiguum	116	$\triangle l/\triangle t =$	0.0006	0.006	0.0001	0.83	0.03

r = correlation coefficient, σ_b, σ_a, σ_r – root-mean-square deviations of the coefficients of the regression equation and the correlation coefficient; σ^2res. = residual dispersion of the regression equation.

Inasmuch as we were interested in the "population" growth of mollusks, we took as a basis the following equation:

$$l = L_{\infty}(1 - e^{-kt}) \quad (2)$$

i.e., Bertalanffy's growth equation.

If the hypothesis is assumed that there is the most possible length L_{∞} (definitive length) for each population, then the equation (2) can be obtained by the integration of the differential equation:

$$dl/dt = k\,(L_{\infty} - l) \quad (3)$$

If instead of infinitesimal increments we write down the final ones, then the equation (3) can be expressed as:

$$\Delta l/\Delta t = k\,(L_{\infty} - l) \quad (4)$$

or

$$\Delta l/\Delta t = kL_{\infty} - kl \quad (4a)$$

Designating $kL_{\infty} = a$, $k = b$, equation (1) is then obtained, the parameters of which are given in the table above. Hence, the equation of the linear growth for *Cerastoderma lamarcki* can be written as:

$$l = 20.88\,(I - e^{-0.0079 \pm 0.0007}) \quad (5)$$

and for *Parvicardium exiguum* as:

$$l = 12.74\,(I - e^{-0.0095 \pm 0.0006}) \quad (6)$$

According to equation (6), the definitive size of *P. exiguum* amounts to $L_{\infty} = 12.74 \approx 13$(mm), which is in good agreement with field observations. Shells of *P. exiguum* longer than 13 mm are very rare. By the end of the first year, yearlings, depending on their hatching time, are 3 to 10 mm in length. By the end of the second year they almost reach their definitive size (11-12 mm) and then grow very slowly. To define the maximum life span by means of Bertalanffy's equation is impossible.

Shells of *Cerastoderma lamarcki* are 4 to 12 mm in length by the end of the 1st year. By the end of the 2nd year, they are 17 to 20 mm in length, which agrees with field observations and literature data. The definitive length for *C. lamarcki* (L = 20.88-21 mm) is sometimes defined less precisely as far as larger mollusks (23-25 mm) occur, but larger specimens are difficult to find and there were very few in the experiment. As a result, the regression equation for *C. lamarcki* (see table) is less precise than for *Parvicardium exiguum*.

Thus, Bertalanffy's growth equation can be obtained if the average growth rate of individuals of different sizes is known. It is not necessary to define their age.

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ENERGY FLOW AND ITS VARIATIONS WITHIN TIME THROUGH POPULATIONS OF TWO SPECIES OF COMMERCIAL BIVALVES ON THE SOUTH COAST OF SAKHALIN

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Abstract

The knowledge of bioenergetics of commercial organisms is quite necessary for elaboration of recommendations on the rational use of organic resources of the continental shelf and for cultivation of economically important species.

The present work deals with the energy flow through populations of *Patinopecten yessoensis* from Busse Lagoon and *Nuculana pernula* from Terpenija Bay.

The calculation of expenditures for metabolism was done by the formula

$$R = (a \cdot \bar{W}^{-b}) \cdot N \cdot K_{(t)}$$

where $\bar{W}$ is an average weight of organisms in the population (in grams); a and b are coefficients (for *Patinopecten yessoensis*, a = 0.35, b = 0.72; for *Nuculana pernula*, a = 0.09, b = 0.71); N = density of colonies in individuals/m^2; $K_{(t)}$ = the temperature correction taken from the Krogh-Arrenius curve. Average temperatures (within a year) of habitats of the populations studied were also taken into account (for *P. yessoensis*, about 17°C in summer, about 5° in spring and autumn, and about 0° in winter; *N. pernula* lives the whole year round at a temperature of about 0°). The caloric value of the raw weight was assumed to be equal to 360 cal/g of raw weight.

Energy assimilated by the populations within a year (A) was defined by the ratio A = P+R (Winberg, 1968; and others), where P is production. The value Ag was estimated as the assimilation necessary for creation of growth production and As is for creation of supporting production.

The coefficient of the effectiveness of the utilization of assimilated food for growth was estimated by the ratio K_{2g} = Pg/Ag. The coefficient of the effectiveness of the use of assimilated food for supporting the population at the energetic level necessary under particular conditions was estimated by the ratio K_{2s} = Ps/As. The bioenergetic potential was defined as Ag/As and served as an index of the population condition.

Expenditures for metabolism in the population of *Patinopecten yessoensis* from Busse Lagoon amount to 18.8 kcal/m^2 per year; its biomass is 16.2 kcal/m^2 (45.1 g/m^2). Annual growth production of this population is up to 5.3 kcal/m^2 per year and supporting production to 4.8 kcal/m^2 per year. Assimilated energy necessary for creation of a growth production of this population accounts for 24.1 kcal/m^2 per year and for creation of supporting production – 23.6 kcal/m^2 per year. The coefficient of the use of assimilated food for the creation of growth production in a population of *P. yessoensis* is equal to 0.22, and the coefficient of the use of assimilated food for the creation of supporting production = 0.20.

The bioenergetic potential of *Patinopecten yessoensis* population is 1.02, which testifies the stationary state of the population.

In regard to the population of *Nuculana pernula* from Terpenija Bay, not only were static indices of the energy flow per year studied, but also their changes in time. The latter is of special interest since in this way we can obtain data on the character and direction of population development.

A 3-fold decrease was recorded, both in the productional abilities and in other bioenergetic indices of the *Nuculana pernula* population from 1947 to 1970. In 1947, the assimilated energy of growth production amounted to 1901.2 kcal/m^2 per year, in 1949 - 2016.2 kcal/m^2 per year, in 1966 – 1115.2 kcal/m^2 per year and in 1970 – 643.8 kcal/m^2 per year. The assimilated energy of the supporting production accounted in the same years for 1670.8, 1806.0, 1039.7 and 620.0 kcal/m^2 per year respectively.

If in 1949 a certain increase in the assimilated energy with a subsequent sharp fall in 1970 was observed, quite another picture took place in the changes of K_2. In 1947 K_{2g} was 0.41, then decreased to 0.37 in 1949 and to 0.28 in 1966. In 1970 this index rose to 0.32. K_{2s} for these years was 0.32, 0.29, 0.23 and 0.29 respectively.

Analysis of the changes in bioenergetic indices has shown that certain fluctuations take place in the energy flow through the *Nuculana pernula* population, which are apparently induced by 11-year cycles of solar activity.

Nevertheless, a general tendency to degradation is observed in the population of *Nuculana pernula*, as evidenced by the changes in the productional (Tabunkov, 1974) and bioenergetic indices. In 1947, the population bioenergetic potential was 1.13, in 1949 it decreased to 1.11, and in 1966 and 1970 it was 1.07 and 1.03 respectively.

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SEASONAL DYNAMICS OF THE NUMBER AND SOME BIOENERGETIC INDICES OF A POPULATION OF *FALSIMARGARITA IRIS* (SMITH) (GASTROPODA: TROCHIDAE) FROM THE DAVIS SEA (EAST ANTARCTIC)

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Abstract

Collections of Soviet Antarctic Expeditions (SAE) conducted off Haswell Island (the Davis Sea) made available vast material, which we could use to analyse the seasonal dynamics of the number and productivity of the populations of marine mollusks from the Antarctic. For a preliminary analysis, we took one of the mass notal antarctic species, *Falsimargarita iris* (Prosobranchia, Trochidae).

A determination of the growth and productivity of the mollusks was made on the basis of an analysis of a size-weight structure of the population and the static and dynamic principle suggested by Golikov (1970). A study of the population structure and its changes in different seasons has shown that the life span of these mollusks is a little more than 2 years. It should be noted that young animals up to 1 year old (about 92%) prevailed in the population and that individuals over 2 years old were rare (less than 1%).

Falsimargarita iris has 2 subgenerations a year, one in summer and one in winter. Mollusks of the winter subgeneration were characterized at early stages of postlarval development by a slower growth rate as compared to the animals of the summer subgeneration; during the first 3 months, individuals of the summer subgeneration grew up to 4 mm, those of the winter subgeneration at the same ontogenetic stages, but undergoing the effect of less favourable factors, grew only to 3.5 mm. In the spring-summer period, the growth rate of mollusks of the winter subgeneration increased and when 1 year old they did not differ in size from those of the summer subgeneration. Individuals of the winter subgeneration are characterized by a shorter life span and do not live to the age of 2 years.

Analysis of the numerical dynamics of the species revealed 2 density maxima of the populations, which coincide with the periods of replenishment of the population with young, taking place in the summer-autumn and the winter-spring periods. It is worthy to note that the increase in the population quantity in the winter period was less than in summer.

Seasonal variations in physical, chemical and biotic conditions caused fluctuations in the density of the species colonies at all depths. Each season except autumn was characterized by an increase in the colonies' density with increasing depth; the highest indices are reported at depths of 33-50 m. The sharpest seasonal variations in the density of colonies were observed at depths ranging from 3 to 15 m. In the summer period, representatives of the species were recorded from a depth of 3 m; at a depth of 8 m they formed aggregations with a density of up to 60 specimens/m^2. In autumn, the upper border of the population shifted to a depth of 6 m. The density of colonies in that period reached 96 specimens/m^2 at a depth of 10 m, and, contrary to the other seasons, a decrease in the density of up to 36 specimens/m^2 (36 m depth) with increasing depth took place. In winter, the upper border of the population shifted up to a depth of 10 m and by spring to a depth of 15 m.

Changes in the density of colonies were accompanied by variations in biomass, which increased with increasing depth. The average annual biomass of the population amounted to 40 g/m^2. The growth productivity of the population, reflecting the weight increment of all individuals of the population for the year, was, on the average, 90 g/m^2. The supporting productivity, providing for the existence of the population under particular conditions at the available age structure, was about 35 g/m^2.

The substance turnover rate of the growth part of the productivity process was 2 times higher than that of the supporting one ($P_{g/B}$ = 2.2; $P_{s/B}$ = 0.88). Such a ratio between the parts of the productional process (Golikov, 1970; Golikov & Menshutkin, 1973; and others) points to a satisfactory state of the population in high antarctic waters.

The estimation of expenditures for metabolism, which was done on the basis of experimental data obtained by some authors in cold waters and on the basis of available information on coefficients of the equation of the respiration dependence on weight, can be written as R = 0.08. W 0.72 cal. and recalculated for the whole population. The average annual expenditures for metabolism were found to amount to 60 kcal. Assimilated energy necessary for growth productivity was 34 kcal/year (assumed caloricity 380 kcal/g of raw substance) and for the supporting production it was 13 kcal/year. The coefficient of the use of assimilated food necessary for growth productivity was found to be equal to 0.35 and for supporting production was 0.18.

The bioenergetic potential of the population, estimated in relation to Ag/As, accounted for 1.29, which suggests a small positive succession of *Falsimargarita iris* in antarctic waters.

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SEASONAL AND ANNUAL DYNAMICS OF THE GROWTH OF THE OYSTER *OSTREA EDULIS* IN THE BLACK SEA

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Abstract

For many years observations have been conducted on oysters of different size (10-90 mm) and age (2-6 years) groups. Oysters were kept in cages at experimental oyster farms in Egorlytzky Bay. The analysis of observations has shown that the growth of oysters is a complex and multiphase process consisting of the growth of the shell and that of the soft parts, with periods of intensified growth alternating with periods of complete cessation of growth in winter. The intensity of growth diminishes with age.

The weight and linear growth rate of oysters over 30 mm in size changed with time (but very little as compared to yearlings), and depended on the abiotic conditions of the environment. The most intensive linear growth was reported for 1966-1967, i.e., for the years characterized by the most favourable temperature conditions (warm winter, early spring warming of the water and even summer temperatures). Minimum linear growth was observed in 1970, which was due to an unfavourable temperature regime. The maximum weight increase was observed in 1969, when the river flow was lower than usual and water salinity was 2 ‰ higher. It should be noted that higher salinity favoured only the growth of valves; the weight of meat did not increase.

Growth of the mollusks takes place virtually only from May to October. In some individuals (10-40 mm in size) growth may begin from the middle of April, but the increase at that time was so small that it could not be estimated confidentially enough. In some mollusks (over 50 mm in size), a negligible increase (more often in weight) was noted in November. The beginning and end of growth depended on the thermal regime of the sea. The value of weight and the linear increase depended to a great extent on a trophic factor.

Analysis of seasonal dynamics of weight and linear increase of oysters has shown that the linear increase in most cases is represented by an unimodal curve with a maximum in July or August. Young oysters in the 10-40 mm size group grew incessantly during the vegetative period. Individuals of older size groups (41-90 mm) grew but little in May; during spawning (June-July) their growth slowed down or stopped.

Curves of monthly weight increase have 2 distinct maxima. The 1st, in July-August, which corresponds to the intensive postspawning linear growth, and the 2nd, less intensive, was recorded in autumn (September to mid-October). In autumn, the increase in the mass of the soft parts of the oysters proceeds, in general, on account of the accumulation of reserve carbohydrates and fats. The cessation of growth and the completion of the annual increase in size are recorded in most cases by the end of October.

Observations of the caged oysters in experimental farms have shown that the linear growth rate of oysters decreases with increase in shell size.

The successive reduction of the value of increments with increasing size permits us to use the equation of the hyperbolic curve, $y = a + \frac{bx}{c + x}$, to express the relationship between the above indices, although this equation has no functional biological grounds. A graphical analysis has shown that empirical points are in good agreement with the theoretical curve.

Analysis of the dynamics of the average annual increment of the total weight in oysters of different size groups has shown that in young oysters a successive rise in weight proceeds with an increase in their size from 11 to 40 mm, and that an increase in weight remains nearly the same in oysters of 41 to 70 mm. It should be noted that the increase in the total weight was observed even in very old individuals (92-95 mm) without an apparent increase in height. This was due to growth in thickness.

Observations on oysters taken from 3 oyster beds have enabled us to establish the general character of growth of all Black Sea oysters and to reveal negligible differences in their growth rate: individuals from Karkintinsky Bay always grow less intensively than those from Dzharylgachsky and Egorlytzky bays. More distinct differences were observed in the growth rate of oysters from various habitats in 1965.

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THE RELATIONSHIP OF SPAWNING OF SOME NORTH CASPIAN BIVALVES TO THE DISTRIBUTION OF THEIR LARVAE IN THE PLANKTON

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Abstract

When investigating the ecology of spawning in marine bottom invertebrates, and in particular the time of onset and the duration of individual phases of the spawning cycle (beginning, duration, maximum of spawning activity, etc.), data are used on the physiological state of adults or on the periods of the appearance and number of their larvae in plankton. These data can be regarded separately or together. In the latter case, due to mutual correction of the data obtained, the evaluation can be, as far as possible, more exact, inasmuch as it is relatively rare to be able to carry out regular observations with the necessary frequency.

Spawning was studied in 7 species of bivalves from the northern Caspian Sea. They were as follows: *Hypanis vitrea, Hypanis angusticostata, Didacna* sp., *Cerastoderma lamarcki, Abra ovata, Dreissena polymorpha* and *Mytilaster lineatus*. Adults were collected from April to October during the years 1968 and 1969. The state of their gonads was studied, the ratio between individuals of different degrees of maturity was estimated, plankton collections were conducted every month and the quantity of larvae of each species was calculated. The time of the onset of spawning, the peaks of maximum spawning, the end of spawning and the general duration of spawning were established.

Peaks of maximum spawning activity of different species of Caspian bivalves which were estimated, on the one hand, by the relative number of fully mature individuals and, on the other hand, by the number of their larvae in plankton, did not coincide as a rule. For most species they were about a month apart. Thus, in *Hypanis vitrea*, the maximum number of adult mollusks was supposed to fall in March (there were no collections in March) and the maximum number of larvae in April; in *H. angusticostata*, in April-May and May-June respectively; in *Didacna* sp., in April and May; in *Abra ovata* and *Dreissena polymorpha*, in May and June respectively; and in *Mytilaster lineatus*, in July and August. Finally, *Cerastoderma lamarcki* had 2 spawning peaks: the 1st one, according to the maximum number of adult individuals, fell in April-May, and according to the maximum number of larvae, in May-June; the 2nd one fell in August and September respectively (in the latter case only a few samples were taken and so the peak is indistinct). This discrepancy can be explained by the following: 1) not all mature individuals start spawning immediately; and 2) identification was done on larvae at the veliconch stage, which, up to the time collected, could have been in the plankton for 2-3 weeks.

Hypanis vitrea and *Didacna* sp. start and finish spawning earlier than do the other species; *Cerastoderma lamarcki* and *Mytilaster lineatus* start and finish spawning later than the others. The total duration of spawning activity was the longest in *H. angusticostata* and *C. lamarcki*; somewhat shorter in *M. lineatus, Abra ovata* and *Dreissena polymorpha*; and rapid in *H. vitrea* and *Didacna* sp. One can judge the rate of spawning activity by the absolute number of larvae. Therefore, during a short mass spawning of *H. vitrea*, the larvae of this species are most abundant in the plankton (8170 specimens/m^3 on the average), while in other species having an elongated spawning period, e.g., *H. angusticostata, A. ovata* and *C. lamarcki*, etc., the number of larvae per unit volume of water is usually lower (maximum 2009, 1778 and 1443 specimens/m^3).

The comparison data on maturity of mollusks and on the number of their larvae in the plankton has shown that after the completion of the spawning season, when no mature mollusks were found in the samples, their larvae stayed in the plankton for a long time (sometimes over a month). Thus, the state of the gonads in adult mollusks points to the end of the spawning season, since larvae make this longer depending on the time of their development. Development under unfavorable conditions can often be abnormally protracted.

The investigation of the distribution of larvae throughout the northern Caspian Sea has shown that at the beginning of the spawning season larvae occurred as separate "spots" and their total quantity was rather low. At the height of spawning, larvae were found everywhere due to their scattering beyond the borders of the colonies of adult individuals, and in a number of places their concentration was rather high. After the completion of the spawning period, larvae occurred throughout a large aquatory, but their number was not high and nowhere did they form high concentrations.

When studying the reproduction of some mollusk species, we had to take into account the possibility of larval drift and the intensity of water warming at the bottom. Thus, the larvae of *Mytilaster lineatus* first appeared in the plankton in the southern part of the northern Caspian in June and July when the water temperature at the bottom is still very low (7-11 °C). It is clear that larvae were brought there from *M. lineatus* habitats off the southern coast of the Mangyshlak peninsula, where coastal waters were already warm enough at this time.

It is evident that the data on larvae require a certain correction which considers the thermal conditions of bottom waters in habitats of populations of adult individuals. Without this, our conclusion on the duration of spawning periods can be erroneous. The above considerations should be taken into account when analysing the spawning regime of any mollusk species.

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NUTRITION OF SOME CASPIAN BIVALVES

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Abstract

Bivalves are widely distributed in the southern and middle parts of the Caspian Sea, where they constitute the main part of the food base – the biomass of mollusks amounts to 70-90% of the total biomass of the zoobenthos.

The feeding of 3 species of mollusks was studied: *Mytilaster lineatus, Syndesmya ovata* and *Cardium lamarcki*. The intestinal content of these species contained, in most cases, detritus, which accounted for 50 to 70% of the total content by weight. This detritus consisted of suspended particles of indefinite form and products of decay of organisms.

In food consumed by *Mytilaster lineatus*, there were found 19 species of algae; in the food of *Syndesmya ovata*, 15 species; and in that of *Cardium lamarcki*, 7 species, of which 3 species, *Exuviella cordata, Grammatophora matina* and *Microcystis grevillei* occurred in food of all 3 species of mollusks. The role of *E. cordata* in the feeding of mollusks is enormous. This alga was found in the intestines of mollusks collected in all sections of the southern Caspian. Quantitatively and in the frequency of occurrence, the 2nd place belonged to *Cyclotella caspia*.

The total number of algal species found in the food of mollusks was 29. Diatoms amounted to 60-75%, blue-green algae to 15-20% and green algae to 10-20%.

An analysis of food content revealed that the intestine of *Cardium lamarcki*, independent of this species' habitats, contained, in general, detritus, and that the intestine of *Mytilaster lineatus* contained algae. This was associated with a poorer development of phytoplankton at the ground surface than in the water mass.

In addition to detritus and phytoplankton, Infusoria play a great part in the feeding of mollusks. Such species as *Coleps tesselatus, Tracheloraphis prennanti, Remanella rugosa, Condylostoma arenarium, Holosticha manca* and *Diaphrys scutum* make, in general, the diet of *Mytilaster lineatus*. These species were found also in the diet of *Syndesmya ovata* and *Cardium lamarcki*.

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COMPARISON OF THE ADAPTATIONS OF MOLLUSKS TO EXTREME AND MODERATE CHANGES IN SALINITY

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Abstract

When conducting ecological-physiological investigations, the tolerance and resistance of the organism in relation to environmental factors are distinguished. In this connection, "capacity adaptation", i.e., in the "tolerance zone", and "resistance adaptation", i.e., in the "resistance zone", are distinguished (Precht, 1958; Prosser & Brown, 1962). In this report, an attempt has been made to analyse the adaptations of the genus *Littorina* to moderate and extreme changes in environmental salinity.

At considerable deviation of salinity from the standard, littorines, like other mollusks, seal the mantle cavity. With less change in the salinity, such a reaction was not observed. The border between these 2 responses falls at different salinities, depending on ecological peculiarities and the functional state of the mollusks being investigated. Further, these responses can be shifted to the side of greater or lesser concentrations of sea water as a result of previous acclimation of the mollusks to increased or decreased salinity.

In the zone of sea water concentrations corresponding to the tolerance range, mollusks behave like typical poikiloosmotic organisms. The osmotic balance with the environment is established some hours

after changes in salinity. Deviations in the salinity from the standard result in the inhibition of respiration, the intensity of which is restored partially or completely within the adaptation process, depending on ecological peculiarities of the mollusks, their functional state and the extent of the effects. Adaptive reactions at the organismal level are determined by adaptational plasticity of cells and tissues, different functions of which become normal after primary breakages caused by changes in salinity. The increase in specific and the decrease in nonspecific cell resistance during the mollusk's acclimation to dissolved sea water are accompanied by the activation of synthesis of RNA and protein and by the reparation of the breakage. At the same time, alternations in the activity of different enzymes take place, as well as changes in their isozymic contents in the mollusk's tissues. Preliminary treatment with inhibitors of RNA and protein synthesis suppresses the ability of mollusks to adapt to salinity. Changes in the activity of the genetic system, which are realized through qualitative and quantitative transformations at the enzymatic level, are supposed to reestablish metabolic processes and their normal course at the new salinity. Cellular functional reconstructions proceed at a great speed. The acclimation processes at the organismal level go slower and their completion requires from several days to 2-4 weeks. The comparison has shown that of White Sea littorins, the most tolerant to salinity is *Littorina saxatilis*; *L. littorea* has a minimum tolerance and *L. obtusata* occupies an intermediate position in this respect. For littorins from the Sea of Japan, the comparative reduction in salinity tolerance can be expressed in the following way: *L. kurila – L. squalida – L. brevicula – L. mandschurica*.

In the resistance zone, other adaptations come to fore, enabling the mollusks to withstand unfavorable salinity for a certain time. The isolating reflex provides the maintenance of an unbalanced osmotic state, during the time the organism is in water, of high or low salinity. Simultaneously with the sealing of the mantle cavity, a sharp inhibition of metabolic processes is observed. This activity is not reestablished up to the death of the mollusk. A quantity of vital dyes absorbed by tissues ultimately reaches high values, which indicates an irreversible alteration of cells. In the zone of transitional concentrations of sea water, the adaptational processes run extremely slow; at extreme changes in salinity, phenotypical adaptation does not proceed at all and the mollusk dies. The survival time of littorins in fresh water depends on a number of morphofunctional characters determining an isolation effectiveness of the mantle cavity from the environment. As a rule, species with a thick shell, well-developed muscular foot and a great store of extravisceral liquid have a greater resistance to fresh water. Among the White Sea littorins, the most resistant is *L. littorea*; among the Japan Sea littorins, *Littorina brevicula* and *L. mandschurica* are the most resistant. A high resistance to a freshening of the medium is usually a result of the general increase in the mollusk's resistance to different abiotic factors, e.g., to drying.

Infection of mollusks with larvae of trematodes reduces the sealing ability of the mantle cavity, and due to this infected mollusks die quicker in fresh water. At the same time, parasites virtually have no effect on the snail host's adaptive system to moderate changes in salinity. Infected and sterile *Hydrobia ulvae* showed the same activity within a salinity fall from 25 to 10-12‰. These data also point to differences in adaptations of mollusks to moderate and extreme changes in salinity.

These differences are reflected in the evolution of littorins. A comparison of the above data with modern concepts on phylogenesis of these mollusks (Golikov & Tzvetkova, 1972) has shown that the evolutionary formation of adaptational complexes to extreme and moderate changes in salinity are carried out independently. Ancestral Pacific species, e.g., *Littorina brevicula*, which have a high resistance to freshening, drying and high temperature, but relatively low tolerance in the ranges of moderate salinity changes, yielded some species withstanding short extreme fluctuations in the habitat conditions so characteristic of the intertidal zone. However, these adaptations are not sufficient for living in brackish waters with a constant low salt content. It is clear that in such a situation, a high metabolic plasticity of cells and tissues, which form the basis of the adaptation to moderate changes in salinity, was evolutionarily more advantageous. This complex of adaptations enabled the descendants of the Pacific species, *L. kurila* and *L. squalida*, to penetrate the brackish waterbodies of the Atlantic.

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ON THE GENERATIONS OF *HYDROBIA ULVAE* (PENNANT) (GASTROPODA) IN THE WHITE SEA

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Abstract

An analysis of data from the literature on the reproduction process in *Hydrobia ulvae* (Pennant) has shown that opinions are contradictory concerning the number and phenology of generations and the life span and growth rate of this mollusk.

During 1969-74, regular observations were carried out on the reproduction of *Hydrobia* from the Kandalaksha Gulf, Chupa Bay (the region of the White Sea Biological Station of the Zoological Institute of the USSR Academy of Science, Leningrad).

A series of shells showing seasonal variation in shell height was obtained. A complete series has 2 distinct chiates, which is indicative of 3 size-age groups (0+, 1+ and 2+ year olds) in the population.

Observations on mollusks of different size-age groupings kept in cages and aquaria have shown that 1) animal growth intensity corresponds to seasonal fluctuations in the size-age structure of the natural population; 2) only 2-year old mollusks spawn; 3) spawning takes place in June-July; 4) 1 *Hydrobia* can lay several clutches; and 5) individuals which gave rise to a generation die, while 0+ and 1+ year old mollusks continue living.

Changes in time parameters of the reproduction process in *Hydrobia* within a distribution area agree with Orton's rule and correlate with a temperature factor. It was known before, and is proved by the author, that in the White Sea *Hydrobia* gives rise to only 1 generation in June-July (Mileikovsky, 1961; Kondratenkov, 1972). However, in September of 1973 we found a spawning population in which approximately 1/3 of the individuals contained clutches. In other populations of the region investigated, the spawning was completed, as a rule, by the beginning of July. It is noteworthy that off East Murman, *Hydrobia* spawns in August-September (Kuznetzov & Matveeva, 1948). A biological explanation of the unusual September generation of mollusks in the White Sea can be based on 2 principally different suppositions: 1) due to weather conditions which deviated from the usual norm in 1972-73, the spawning period was of longer duration (June-September), or it shifted from June to September, or the 2nd generation appeared in September, i.e., the phenomenon has a character of phenotypical variability; or 2) the September generation in this population, as in *Hydrobia* from East Murman, was normal, i.e., was more rigidly determined genetically.

Depending on the confirmation of any of the above suppositions, we shall be able to give a valid substantiation of the level of intraspecies heterogeneity in the White Sea *Hydrobia*.

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PECULIARITIES OF THE GENITAL SYSTEM OF THE RISSOACEA AND THEIR IMPORTANCE FOR TAXONOMY IN THIS SUPERFAMILY

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Abstract

In the process of evolution of the Rissoacea, a genital system was formed typical for Monotocardia, which consists of 5 general parts: gonodial, renal, bursal, pallial and cephalopodial (Minichev & Starobogatov, 1971b). A distinct tendency for a substitution of the renal and bursal parts with a younger pallial one makes the homologization of some portions of the genital system difficult and prevents the elucidation of relations within this taxonomically very intricate superfamily.

Morphological studies of the following marine Far Eastern Rissoacea (*Thapsiella plicosa, Barleeia angustata* and *Falsicingula athera*) have enabled the author to establish their taxonomic status and to

define more precisely the homology and origin of some portions of the genital system.

Due to the peculiarities of the morphology and topography of the seminal pouch of the oviduct, we can give a distinct definition of these additional organs. The seminal receptacle is always connected with an albumen gland, forming a fertilization pocket. It opens either into a glandular cavity (in *Alvania, Rissoa inconspicua, R. hamiltoni* and *Barleeia angustata*) or into its duct (in *Thapsiella plicosa*). Its cavity is lined with a cuboidal epithelium and is enveloped with musculature from the outside. Apparently the seminal receptacle is formed from the material common with the albumen gland and can be both renal and pallial in its origin.

The bursa arises independently from the mantle roof. Its duct opens initially near the primary genital orifice at the hind end of the mantle cavity. Bursae situated on the distal and proximal ends of the pallial oviduct are not homologous with each other. The disal bursa of *Rissoa inconspicua* and *R. hamiltoni* opens near the secondary genital orifice. It arises in the shape of the pouch of the vaginal duct and serves for acceptance of the sperm. A proximally situated bursa in most Rissoacea (including *R. inconspicua* and *R. hamiltoni*) performs a function of the gametolitic gland (according to the terminology of Thompson & Bebbington, 1969). Having lost an independent entrance into the mantle cavity, it has aequired an ability for the resorption of surplus sperm. Its epithelium is formed by high glandular cells filled with a homogenous secretion containing decayed spermatozoa. Similar formations can appear on account of the renal part (*Barleeia angustata*) and pericardium (*Falsicingula athera* and *Thapsiella plicosa*).

As far as the gonopericardial duct is a homologue of the renopericardial connection of the right kidney, it should be regarded as a conventional border between the renal and pallial parts. *Falsicingula athera* and *Thapsiella plicosa* have preserved this duct, and the pericardium functions as a gametolitic gland. In *F. athera* the renal part is short and lacks appendages. The gonopericardial duct in *T. plicosa* is connected with the oviduct near the bursal duct. The renal part is long and bears an albumen gland and a seminal receptacle. Such structures of the oviduct are characteristic of the Onobidae, Rissoidae and Rissoinidae, but the gonopericardial connection is lacking. The males of *T. plicosa* have a pallial prostate, as do the males of the Onobidae. In the Rissoidae and Rissoinidae, the prostate is situated in the cephalopodial part (in the copulative organ). On this basis, *T. plicosa* should be removed from the family Rissoidae and placed in the family Onobidae. Due to a peculiar structure of the pallial part in *Falsicingula*, the genus can be separated into a distinct family (Slavoshevskaya, 1975).

In females of *Barleeia angustata*, the albumen gland is situated in the pallial rather than in the renal part and represents a differentiated portion of a single glandular oviduct with a central duct. The renal part is formed by the gametolitic gland, which opens into the pallial part at the bursa level. The bursal part is preserved in its initial state. It consists of the reservoir, with a duct independently opening into a hind end of the mantle cavity. Both reservoir and duct are formed by ciliate epithelium with scattered mucous cells. The 2nd ovisac is clearly pallial in its origin, since its epithelium gradually passes into the epithelium of the albumen gland of the pallial oviduct. In the males of *B. angustata*, the prostate gland is located in the penial duct, while in *B. rubra* it is pallial.

Taking into consideration the difference of *Barleeia angustata* from all the other Rissoacea, we erected the genus *Ansola* for this species. This genus is characterized by a small, smooth shell, an operculum with a process, a wide foot with a longitudinal furrow on the sole, the absence of caudal and pallial tentacles, eyes in the base of small tentacles, and by direct development. The type species is *Assiminea angustata* Pilsbry.

Analysis of the structure of genital systems in marine Rissoacea suggests the following groups of species which we regard as distinct families. (Aberrant and little-studied species are excluded.)

1. The pallial part in females is represented by 1 gland and a non-isolated ventral ciliate groove. The renal part consists of the compact gland with a ciliate duct. The male pallial part is non-glandular, and the prostate is in the cephalopodial part.

Rissoidae Gray 1847: *Mohrensternia parva* Costa, *Rissoa violacea* Desmarest, *Rissoa membranacea* (Adams), *Rissoa lilacina* Recluz, *Cingula cingillus* (Montagu).

2. The pallial part in females is formed by 1 gland and an isolated ventral ciliate canal. The renal part is a glandular duct curved without an isolated gland. The pallial part of males has a distinct prostate.

Alvaniidae Golikov & Starobogatov 1972: *Alvania reticulata* (Montagu), *A. subsoluta* (Aradas).

3. The female genital system is arranged in the same way as in the Rissoidae and differs only in the structure of the ventral canal, which forms a small fold separating a glandular portion of the oviduct from the ciliate one. The prostate gland is in the pallial part.

Onobidae Golikov & Starobogatov 1972: *Onoba semicostata* (Montagu), *O. semistriata* (Montagu), *Arsenia punctura* (Montagu), *Thapsiella plicosa* (Smith).

4. The pallial and renal parts of females bear only 1 gland. The ventral ciliate canal passes into the vagina which is provided with a copulatory pouch. The genital system of males is of the same type as in the Onobidae, but the penis is provided with a filament.

Haurakiidae Slavoshevskaya 1976: *Haurakia hamilton* (Suter), *Rissoa inconspicua* Alder.

5. The single glandular pallial oviduct with a central duct is distinctly differentiated into 2 glands.

The renal part is short, lacks appendages and is connected with the pericardium, which functions as a gametolitic gland. The pallial part in males has a well-developed prostate gland.

Falsicingulidae Slavoshevskaya 1974: *Falsicingula athera* (Bartsch), *F. kurilensis* (Pilsbry).

6. The pallial part in females is formed by a glandular epithelium, which is histologically differentiated into 2 glands with a central duct. A long renal part functions as a gametolitic gland. The bursal part opens independently into the hind end of the mantle cavity. The prostate is in the cephalopodial part.

Ansolidae Slavoshevskaya 1976: *Ansola angustata* (Pilsbry).

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TAXONOMIC POSITION AND ECOLOGY OF BLACK SEA HYDROBIIDAE

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Abstract

The purpose of this paper is to elucidate the taxonomic status and the species of Black Sea hydrobiids. With this aim in view, a study of shell variability and functional morphology was undertaken, using serial sections cut with a microtome. The spawning of Black Sea hydrobiids, the sex ratio, reproduction periods, and the character of ovogenesis and egg laying were studied. The growth of hydrobiids was studied through analysis of histograms of population size groups and observations in tanks.

All Black and Azov Sea hydrobiids are characterized by a common pattern of structure. The female genital system has 2 sperm sacs, a large copulatory pouch and a small seminal receptacle. In the cavity of the pallial oviduct, there is a large longitudinal fold separating a vaginal canal. The presence of a spirally curved dark renal oviduct is a characteristic feature of hydrobiids. Consequently, these mollusks must be assigned to the family Hydrobiidae.

The populations of Black Sea hydrobiids are characterized by great shell variability. An ecological variability associated in general with depth, age variability, sexual dimorphism and parasitic gigantism can be distinguished.

The Black Sea and Azov Sea hydrobiids have 2 types of development: 1) small eggs from which pelagic larvae develop; and 2) large eggs, without pelagic larvae. A hydrobia with a non-pelagic development can be identified as *Hydrobia ventrosa* (Mont.) and a hydrobia with a pelagic larva can be identified as *H. acuta* (Draparnaud). From hydrobia having a direct development, another species can be recognized, *H. pusilla* (Eichw), differing from *H. ventrosa* in shell shape and reaching larger sizes. The species is apparently an endemic of the Azov-Black Sea and Caspian basins.

A mollusk very similar to *Hydrobia* in the shape of shell, foot, head and radula, but utterly different in the structure of the genital system was found off Sevastopol. In the Black Sea, this mollusk has a very limited distribution, but it occurs in great quantity. In contrast to hydrobiids, the longitudinal fold separating the vaginal canal is missing from the pallial oviduct cavity; it is represented by a simple slit. The renal oviduct is rather short and light, and does not form a dark pigmented curved spiral as in hydrobiids. The male genital system also differs to a great extent. In contrast to hydrobiids, this mollusk lays compact leathery cocoons not covered with grains of sand or detritus. It has a direct development, without a pelagic larva. We named this mollusk *Falsihydrobia streletzkiensis* Chukhchin 1976. It is difficult to refer this species to a family. In the structure of the female genital system, it is close to the families Assiminaeidae, Barleidae and Cingulopsidae; the species is very close to *Falsicingula elegans*, whose genital system was studied by Lazareva (1971) and Slavoshevskaya (1975). However, the species has a duct connecting the oviduct with the mantle cavity, which is absent in *F. elegans*.

Most individuals in the *Falsihydrobia streletzkiensis* population were represented by females, the number of males amounting to only 0.5% (in populations of hydrobiids, the sex ratio is close to 1:1). The sex ratio and development of this mollusk shows that its reproduction is parthenogenetic. During maturation of the egg, 2 polar bodies are produced, and parthenogenesis is haploid in character. In addition, *F. streletzkiensis* is a polyploid species.

The life cycles of *Hydrobia acuta, H. ventrosa, H. pusilla* and *Falsihydrobia streletzkiensis* are similar in common features. These species have annual life cycles.

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SOME PECULIARITIES OF THE DISTRIBUTION AND ECOLOGY OF BIVALVES FROM TONKIN BAY

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Abstract

Bivalves collected by the Soviet-Vietnamese expeditions in Tonkin Bay and Bivalvia collected by the scientific workers of the Zoological Institute in the intertidal zone of Hainan served as a basis for the present investigation. In all, 3,800 samples containing over 11,000 specimens were examined; 253 species belonging to 108 genera and 24 families were identified.

The species can be arranged into 10 groups according to their types of distribution.

1. Indo-West Pacific group, in a broad sense. This group includes 37 species, i.e., 14.6% of the total number of species. It corresponds to the Indo-West Pacific elements of the Tonkin Bay fauna as distinguished by Gurjanova (1972) and it is connected in origin with the Tethys Sea.
2. Indo-West Pacific group, excluding Oceania. This group consists of 50 species (19.8%).
3. Amphi-Indo-West Pacific group. This group includes 20 species (7.6%). It should be noted that the disconnected distribution might be only apparent, being due only to our insufficient knowledge of the Indian Ocean fauna. Two latter groups correspond to West Atlantic-Indian elements of the Tonkin Bay fauna (Gurjanova, 1972).
4. East Indian-West Pacific group. This group includes 27 species (10.7%).
5. West Pacific group, including Oceania. This is a small group, consisting of only 3 species (1.1%).
6. Japanese-Australian group. Twenty-five species (9.9%) have such a distribution.
7. Philippine-Malayan group. This group includes 16 species (6.3%).
8. Japanese-Malayan group. This group has 31 species (12.2%).

The 5 latter groups correspond to the eastern or the Philippine-Malayan elements of the Tonkin Bay fauna (Gurjanova, 1972), having their developmental centre in the Philippines and the Malay Archipelago, thus having penetrated the west only up to the Bay of Bengal. Accordingly, the Philippine-Malayan elements are represented by 103 species (39.2%).

9. Chinese-Japanese group. This has 37 species (14.6%). It corresponds to the Sino-Japanese elements of the Tonkin Bay fauna and is formed by autochthonous species of southern Japan which have spread to the south along the eastern continental shelf of Asia.
10. Conventional endemics from Tonkin Bay; these are 7 species (2.4%).

An analysis of the fauna of littoral and sublittoral mollusks has shown that their biogeographical characteristics are very close. Among sublittoral mollusks, there is a greater number of species with wide distribution areas which embrace either the whole Indo-West Pacific or only its eastern part, or are widely distributed in the Western Pacific (57.1% of the sublittoral species, as compared to 50.8% of littoral ones). Among inhabitants of the littoral zone, those mollusks which are more abundant are limited in their distribution by the coasts of China and Japan (16.7% against 12.8% of sublittoral species).

The formation of the Tonkin Bay fauna began as early as the Late Pleistocene, when a direct exchange of faunas became possible between tropical regions of the Western Pacific and the southeastern part of the Indian Ocean. This fact, apparently, can explain a considerable number (134 species, i.e., 54%) of common species of bivalves in Tonkin Bay and in the Indian Ocean of the Indo-West Pacific superregion.

A comparison of the species composition of the bivalve fauna from Tonkin Bay with that from coastal waters of the Philippines and southern Japan has shown that the malacofaunas of Tonkin Bay and waters washing southern Japan are more similar than those of Tonkin Bay and the Philippines. Indeed, the similarity factor estimated by the formula of Jaccard-Alekhin amounts in the first case to 39% and in the second case to 22%. The difference factors according to Preston were 0.51 and 0.66, respectively. The faunas of bivalves from the littoral zone of the northern part of Tonkin Bay and Hainan have still greater similarities. The similarity factor according to Jaccard-Alekhin is 48.7% and the difference factor according to Preston is 0.39 (20.6% of the total species from their summary quantity). Thus, a conclusion can be drawn that the fauna of bivalves from Tonkin Bay is a united tropical Indo-West Pacific fauna and can be included in the Hainan province (separated by Gurjanova, 1972) of the Sino-Japanese subregion of the Indo-West Pacific superregion.

A biogeographical analysis of bivalves from Tonkin Bay and coastal waters of Hainan has shown that 67 species, i.e., 26.4% of the total number of species studied, are typically tropical. Their areas do not go beyond the ranges of tropical waters and thus the temperatures of survival and temperature optima for these species as determined by Golikov & Scarlato's (1972) method were close to each other and accounted for 20-29° and 25-28°C respectively. However, the main part of the fauna of bivalves from

Tonkin Bay is formed by tropical-subtropical species – 181 (71.6%), whose distribution areas enter subtropical waters. They can be arranged into 2 groups, the larger of which includes species distributed northwards to Sagami Bay, Honshu. This group consists of 170 species; temperatures of survival are in the range of 15-29°C and the temperature optimum in the range of 15-26°C. The 2nd, smaller group consists of 11 species. Their distributions are similar to those of the species from the 1st group. However, they are reported from the Yellow Sea, and due to this, these mollusks have a wider range of survival temperatures, 5-29°C, and nearly the same temperature optimum, 15-25°C. Five species (1.9%) are distributed up to low boreal waters (Peter the Great Bay, coasts of southeastern Sakhalin and Hokkaido). Survival temperatures of these species lie in the limits from 0 or even -1° to 29°C, and the temperature optima from 15-20° to 17-22°C.

One hundred twenty species were found in the littoral zone, but some of them inhabit the upper littoral as well. One hundred thirty-three species are confined only to the sublittoral. Analysis of the available material showed that the greatest number of sublittoral species occurs at a depth from 20-65 m; only 16 species go beyond the 100-m isobath, and only 6 species are reported from a depth of 150 m.

The maximum variety of bivalve mollusks in Tonkin Bay was recorded from mixed grounds, on which 63.5% of all species studied live; 13.5% are characteristic of hard grounds (coral reefs, rocks); 15% live on a sandy ground; and only 8% are adapted to mud. The majority of the species are representatives of the infauna.

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ADAPTATIONS TO EGG BEARING IN SOME MARINE BIVALVES

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Abstract

Most marine bivalves lay mature genital products into the water, where fertilization and further development of the embryos take place. Due to such a mode of reproduction, the extinction of eggs and embryos is especially great, which is compensated for by the extremely high quantity of gametes. However, some species possess a number of specific adaptations protecting developing embryos from the influence of unfavourable environmental factors, thereby increasing considerably their survival rate. Mollusks possessing such adaptations occur in different, often rather remote families.

One of the simplest adaptations, larva viviparity, is observed in members of the family Ostreidae. Individuals of this family discharge only sperm into the water; eggs are maintained by females in the pallial cavity, where fertilization occurs with sperm coming into the shell with the water flow. Embryos develop in the cavity within 8 days and enter the water as free-swimming larvae. In this case, the adaptation manifests itself at an early ontogenetic stage; mortality of eggs decreases, thereby affecting the effectiveness of fertilization.

In members of the family Astartidae, the females spawn large eggs (up to 300 microns) with 2 protecting jelly membranes. A small number of eggs rich in nutritive yolk defines a principally new character of embryogenesis. Such widely distributed species in Arctic waters as *Astarte borealis, A. elliptica* and *A. montagui* are characterized by a rapid development of embryos and the lack of pelagic larvae. The direct development decreases the death of embryos and increases considerably the quantity of progeny.

Among bivalves there are species producing clutches. In the family Veneridae, *Turtonia minuta* is such a species, forming masses of colonies in the littoral zone. The females lay fertilized eggs into transparent clutches, attaching them with byssal threads to the substratum. The clutches contain from 1 to 25 relatively large eggs, which have a direct development. In the family Mytilidae, representatives of the genus *Musculus* (e.g., *M. discors, M. laevigatus* and *M. senhousia*) have clutches. These mollusks attach themselves with their byssal threads to the thalli of algae, thereby forming around the shell a peculiar house into which the females lay their clutches, which are in the shape of white twisted cords consisting of large eggs sticking together. The first 2 species have a direct development; in *M. senhousia* veligers hatch from clutches, which for a short time develop in the plankton and after completing metamorphosis settle on algae. As a result of investigations carried on by the author off the Kuril Islands, the females of *Vilasina pillula* (Mytilidae) were found to produce clutches which represent roundish mucous clots of

greenish-grey color 12 mm in diameter. The external membrane consists of interlacing brown filaments of the byssus, stuck together by stroma and covered by a thin layer of detritus. In July there was a great number of developing larvae at the veliger stage inside the clutch in the transparent stroma. We suggest that in a given case embryos of this species have a direct development or a very short planktonic stage.

Some species of bivalves bear eggs in a special sac attached to the shell. Such an adaptation was found in *Nucula delphinodonta* of the family Nuculidae. The sac is formed of a leathery material connected with the mantle cavity and contains from 20 to 70 eggs. The eggs are large (the average size is 210 microns), non-transparent, brownish, and have direct development.

Ovoviviparity is a further step in the complication of reproduction. In most Pacific species of the family Carditidae, eggs and embryos develop under protection of the shell. Thus, in *Cardita ventricosa, C. barbarensis* and *C. bailui* there are from 20 to 50 embryos in the spaces of the demibranches. In the egg membranes, the embryos have the same developmental stages as in the plankton. Females with embryos inside the shell were found in the population the whole year round, excluding June. Ovoviviparity was observed in *Cardium elegantulum* also. The females of this species lay developing eggs in 2 special brood pouches formed by ventral folds of the mantle. The embryos have a direct development, without planktonic larvae, and develop both under the protection of the shell and inside the brood pouches.

Thus, the adaptations associated with egg-bearing were observed in bivalves at different ontogenetic stages from early egg and to subsequent embryonic stages. All morphophysiological adaptations connected with this are directed to the improvement of forms and modes of reproduction, thereby providing embryos with reliable protection from unfavourable factors. The tendency for morphophysiological adaptations oriented towards the preservation of eggs and embryos manifests itself at the family level and is realized in species with small shells or in species living under unstable and severe environmental conditions. The most important adaptation to the protection of progeny is the yolk content in the egg. Large eggs, yolk-rich and few in number indicate the direct development of embryos in most cases.

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ON THE REPRODUCTION OF *ACTEONIA COCKSI* (ADLER & HANCOCK) (OPISTHOBRANCHIA: SACOGLOSSA) IN THE INTERTIDAL ZONE OF THE KANIN-NOS PENINSULA

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Abstract

Only 1 species of Sacoglossa, *Limapontia capitata* (Müller), was recorded previously from the northern seas of the U. S. S. R. In June-August 1972, we observed adults of another sacoglossan, *Acteonia cocksi* (Adler & Hancock), in great numbers in tidepools of Charlov and Ainov islands and Dalnije Zelentzy (Barents Sea). Single specimens of *A. cocksi* were located in 1973 in the intertidal zone of Sosnovets Island (White Sea) (Roginskaya, 1976). The external morphology and color of both species mentioned are extremely similar, except for the head region. The head of *A. cocksi* bears a pair of laterally projecting minute oral tentacles, which are lacking in *L. capitata.*

The egg masses of *Limapontia capitata* contain up to 450-900 small ova (67-100 μ in diameter) and the veligers are provided with spiral larval shells (Thorson, 1946; Chukhcin, 1960; Chia, 1970). The embryonic period of *L. capitata* includes a long planktonic swimming phase. Direct development is exhibited by *Acteonia cocksi* (Pelseneer, 1899).

Egg masses of *Acteonia cocksi* were not found in 1972 or 1973, so therefore we could not observe directly the development of this species in the field or in the laboratory. A histological study of gonads of *A. cocksi* revealed ovarial ovocytes of great size, characteristic of direct development. In July 1974, in small, shallow, intertidal pools on the rocks of Kanin-nos Peninsula, not only adult specimens of *A. cocksi* were detected, but also their round or oval, transparent, jelly-like egg masses (3 x 2 mm in size) were collected among tufts of filamentous algae. Each egg mass contained up to 30 large bright yellow ova (160-200 μ in diameter), coated in transparent egg capsules (400 x 300 μ in size). Since the depth of the small, high, intertidal pools populated with *A. cocksi* reached only 4.5-15 cm, the water temperatures can

rise to 16-22°C during the period of low tide, when the rock pools are exposed to the sun for at least 6-8 hours on sunny days.

Similar to populations of *Acteonia cocksi* from England and Belgium, the whole developmental period of Kanin-nos specimens occurs within the egg mass. During embryonic development, the larval velum and foot differentiate, although the larval shell does not appear on the embryo. Gradually granules of black pigment accumulate in the skin of the veliger, so that hatching, crawling juveniles exhibit the body pigmentation pattern of adults (black dorsal side, whitish area around the eyes, whitish abdominal side). The juveniles differ from the adults externally only by their dimensions (0.8-0.9 mm in length). The maximum length of adults from Charlov Island is 8.5 mm; the largest Kanin-nos Peninsula specimens of *A. cocksi* were 6.2 mm. Hatching of *A. cocksi* started in the field around the 20th of July. We could not check mass hatching of this species in nature because observations were interrupted. At that time the early egg masses comprised 59.3%, the egg masses with pigmented veligers 25.3% and the empty egg masses 15.5% of daily samplings.

The very striking external similarity of *Limapontia capitata* and *Acteonia cocksi* and their identical habitats often have led to misidentification of these 2 species, especially as the degree of tentacle development (the characteristic feature of *A. cocksi*) changes with age and state of the mollusk. Tentacles are practically indetectable in preserved specimens. Therefore we cannot completely reject the possibility that the records of *L. capitata* made by Herzenstein (1885, 1893), Derjugin (1915), etc., on the Murman coast may be wholly or partly attributed to *A. cocksi*. This opinion is supported by our abundant findings of *A. cocksi* and the complete absence of *L. capitata* when investigating the intertidal zone of the Murman coast. All specimens in the collection of the Zoological Institute of the Academy of Sciences of the U. S. S. R. identified by N. I. Volodchenko as *L. capitata* proved to be *A. cocksi*.

The single indication of the presence of *Limapontia capitata* in the White Sea are the data from the paper of S. A. Mileikovsky (1958), who was successful in procuring the metamorphosis of larva (which were identified by him as *L. capitata*) from Great Salma Strait. Recently, a 3rd species of Sacoglossa new for Soviet northern seas, *Alderia modesta* (Loven), was determined by me from Dalnije Zelentzy (collection of Z. I. Kobjakova). The veliger of *A. modesta*, which is provided with a black ring of pigment around the mouth, a black stripe on each velar lobe and a black anal gland (Seelemann, 1967), is very similar externally and in dimensions to the picture of the *L. capitata* veliger presented by Mileikovsky in the work mentioned above.

The problem of the species composition of Sacoglossa in the northern seas of the U. S. S. R. needs more precise definition. For the present, we must include 3 species in the list, *Alderia modesta*, *Acteonia cocksi* and, doubtfully, *Limapontia capitata*.

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SOME ECOLOGICAL AND MORPHOLOGICAL PECULIARITIES OF THE POPULATIONS OF *MYTILUS EDULIS*

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Abstract

The formation of 3 populations of *Mytilis edulis* in ontogenesis is analysed, a Japan Sea population (Popov Island, Peter the Great Bay), a Pacific Ocean population (Spasenija Bay, Avatcha Bay) and a North Sea population (Yorkshire, Great Britain; Seed, 1968). The main material was collected in the Sea of Japan in different seasons and habitats. The effect of artificial and natural substrata and the force of turbulence on the relative indices of size and weight of littoral-upper sublittoral animals was studied. A dependence was established between the height (H), width (S), dry weight of soft tissues (Wm) and shell (Wr) to the length of the shell (L). Japan Sea mollusks from rocks and piles used for moorages, independent of the force of turbulence, were characterized in spring and autumn by allometric growth, which can be expressed as $y=ax^b$, where the exponents $b<1$ for dependencies H(1) and S(1) are ~ 0.87 and ~ 0.97, respectively, and where the exponents $b<3$ for dependencies Wm(1) and Wr(1) are ~ 2.77 and ~ 2.84, respectively. In summer, the dependence S(1) changes – the width becomes the more quickly growing parameter (the exponent is ~ 1.08). Young and mature individuals living on algae can have isometric growth. The ratio Wm/Wr was the least in animals from rocky capes with rather high turbulence

(15% on the average, and 24% in *Mytilus edulis* from piles).

Pacific *Mytilus edulis* (collected only in summer) from the wall of a dock had the exponents for H(1) and S(1) ∿0.89 and ∿1.07, respectively; from rocky grounds ∿0.88 and ∿0.97, respectively. The ratios of Wm/Wr for H(1) and S(1) were 18% and 11%, respectively.

A recalculation of Seed's data has shown that in *Mytilus edulis* from stony grounds in the North Sea, the shell width was the most quickly growing parameter (the exponent in the dependence of S(1) was 1.11), and the ratio Wm/Wr was about 8%.

Therefore, the distinct differences between the populations in question are expressed by the ratio between soft and hard tissues, the Pacific and Japan Sea animals preserving the tendency for a decrease in the value Wm/Wr on natural substrata as compared to artificial substrata.

It is possible that *Mytilus edulis* of both populations from Soviet waters differ from the Yorkshire ones in shell shape.

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A PARTICULAR CASE OF ALLOMETRY IN THE COCCULINIDAE (GASTROPODA: PROSOBRANCHIA) AND ITS USE IN THEIR TAXONOMY

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Abstract

About 60 Cocculinidae species have been described during the last 100 years. These mollusks often inhabit substrates of extra-benthic origin, such as submerged pieces of wood, fruits, etc. They have wide ranges of geographical and depth distribution, occurring from sublittoral to ultra-abyssal (hadal) zones. Such peculiarities in the mode of life and distribution of Cocculinidae made the study of these mollusks very meaningful for constructing theories of zoogeography and general biological structure of the oceans of the world. At the same time, criteria for discrimination of genera in the family are now poorly developed. The family is subdivided into only 4 taxa of the rank of genus (*Cocculina, Coccopygia, Pseudococculina* and *Dallia*). Such a situation is not satisfactory. The same is true concerning systematics at the species level. A uniform pattern of species description has not been developed, and the diagnostic values of certain characters have not been investigated, as well as their permanence in individuals of different size and age.

The investigation of allometry was undertaken to evaluate the diagnostic significance of shell proportions. Length (l), width (s), and height (h) of the shell were measured in 27 specimens of species "E", and in 177 specimens of species "A", which are most abundant in the collection of the Institute of Oceanology. The observed h-values showed considerable error because of the technique of measurement. For this reason only l and s values were used. The regression coefficients of log s on log l did not differ significantly from 1 in both cases. Thus, we have here a particular case of allometry where the proportions remain the same in a growing animal. The s/l ratio is independent of the size of the shell and may be regarded as a discriminative character if its specific values differ significantly. According to the method of Snedecor (1958), the infraspecific s/l ratio was calculated as regression coefficients of s on l.

The figures were 0.642 and 0.720 for species "E" and "A", respectively. The standard deviations were 0.01527 and 0.05779, and the "F"-test gave significant differences between variances ($F = 14$, d.f. = 25 and 200). The character "s/l ratio" was more variable in species "A". Taking into consideration the difference in variances, we compared the mean values of the s/l ratio, using the Student's test. In this case $t = 18$, d.f. = 115, $p < 0.001$.

Thus, it is possible to conclude that (1) the s/l ratio is independent of the size of the shell, and (2) the difference of these values between species "E" and "A" is significant enough to use the s/l ratio as a specific discriminating character.

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NUTRITION OF THE SHIPWORM *TEREDO NAVALIS*

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Abstract

Until now there has been no common opinion as to the food of shipworms, and only recently a conclusion has been drawn that these mollusks eat both wood and seston. Quantitative aspects of *Teredo* feeding have not been studied. The purpose of the present investigation was to determine the daily diet of Black Sea *Teredo navalis* under laboratory conditions and in nature.

The work was done in the Southern Department of the Institute of Oceanology, Academy of Sciences, U. S. S. R. (Rybatskaya Bay) in July-August, 1972. Pieces of wood with shipworms were used in the experiments. The pieces were kept in the sea for about a year, then cleansed of foulings, washed with sea water and maintained for about 24 hours. Then they were transferred into reservoirs with filtered sea water, where, after washing for Cystozeira, water was added (thin fractions of wood were used which did not sink for a long time). The feeding intensity was determined by the quantity of excrement excreted by the animals within 24 hours. The duration of each experiment was 10-14 days. Each day, water and food were changed in the reservoirs and feces (of each size group) were collected. Fifteen experiments were conducted with animals ranging from 0.72 to 38.6 mg in dry weight. As a result, the values of non-assimilated food excreted by the animal for 24 hours were obtained. Diets were calculated by the equation $R = H/1\text{-}U^{-1}$, where R is the diet, H is the quantity of non-assimilated food, and U^{-1} is assimilability. The latter has been accepted to be equal to 0.65 for energetic values and 0.60 for weight values. Caloricity of feces and animal tissues was determined by the wet combustion method.

The feeding intensity of *Teredo* in the laboratory and in the sea was compared by the quantity of feces excreted by the animals. With this aim in view, the samples just brought from the sea and those kept for 2 weeks in the laboratory were maintained for 5 hours in pure filtered sea water; the feces collected were dried and weighed.

Parameters were calculated in the regression equations connecting the weight of the animals (w) or its energetic equivalent (W_1) with weight (H) or energetic equivalent (H_1) of the quantity of excreted non-digested food. This equation can be expressed as $H = 0.181w^{0.66}$ for weight units, and $H_1 = 0.235w_1^{0.61}$ for energetic units. A difference in the values of exponents was caused by unequal caloricity of *Teredo* of different weights.

It is known that the exponents in equations describing the dependence of the quantity of consumed and non-digested food on animal weight has similar or close values. That is why, when calculating parameters of the equation of the dependence of the diet on *Teredo* weight, the exponents were assumed to be equal to 0.66 (weight units) and 0.61 (energetic units). In regard to the coefficient "a" describing the intensity of process, it (as is known from the balanced equation) is equal to an analogous coefficient in the dependence of the non-digested food quantity on weight divided by $(1 - U^{-1})$. Consequently, $a = 0.181 : (1 - 0.60)$ (weight units) and $a = 0.235 : (1 - 0.65)$ (energetic units).

The equation describing the dependence of diet on weight can be expressed as $R = 0.452w^{0.66}$ (weight units) and $R_1 = 0.67w_1^{0.61}$ (energetic units). Relative average daily diets in the ranges of the weights investigated decreased with increasing animal weight and stayed in the limits from 50% (animal 1 mg in weight) to 10% (animal 40 mg in weight).

Data on relative average daily diets of marine bivalves are rather scanty. Calculated relative average daily diets in *Macoma baltica* (according to Bubnova, 1971; Khmeleva & Sans, 1966) are somewhat lower than those in *Teredo*. This, apparently, is due to the rudimentary shell of *Teredo*.

We compared the intensity of feeding of *Teredo* in the laboratory and in the sea by the method described above. In the sea, after a 2-week maintenance of the animals in the laboratory, shipworms were found to excrete virtually the same quantity of feces, 5.7 and 5.2 mg respectively. Consequently, laboratory conditions do not affect the feeding intensity of *Teredo*. An opinion has been expressed on the 2-fold increase of the diet in nature as compared to that of laboratory conditions. We believe that food contents play a great part in this. The fact is that in the laboratory it is practically impossible to choose just the same food which the animals consume in a natural body of water. That is why certain corrections should be made for "laboratory data" by the method described by us for *Teredo*. Apparently, the identity of diets of *Teredo* in the laboratory and in the sea is not a rule. It can be explained by properly chosen laboratory food.

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DISTRIBUTION OF MOLLUSKS OF THE GENUS *NEPTUNEA* IN THE BERING SEA

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Abstract

Mollusks of the genus *Neptunea* Bolten are the largest gastropods in the seas of the U. S. S. R., and 9/10 of all known *Neptunea* are recorded from the seas of the U. S. S. R. In the monograph by Golikov (1963) dealing with *Neptunea*, there were exactly defined boundaries between species and their synonymies were specified.

According to Golikov, 11 species of *Neptunea* occur in the Bering Sea. However, investigations conducted in the Bering Sea in 1972-73 confirmed the presence of only 7 species of this genus there. *Neptunea varicifera* var. *costulata* (= *N. soluta* var. *costulata*) was not recorded in this region. Instead, *N. laticostata ochotensis*, which was not previously reported for the Bering Sea, was found in abundance. *Neptunea insularis* was not found, apparently because of its low quantity and confinement to the edge of the continental slope. The occurrence of *N. oncoda*, *N. vinosa* and *N. smirnia* in the Bering Sea is doubted.

The uneven distribution of *Neptunea* in the Bering Sea is defined by definite regularities. Sites where these mollusks accumulated were found near the outlets of the bays of the Bering Sea (Bristol, Anadyr, Karaginsky and Norton Bays) and in the central part of the sea near the edge of the continental slope. These accumulations are, apparently, temporary in nature, since *Neptunea* are actively moving predators-scavengers and their confinement to definite biocoenoses is rather doubtful.

Unevenness in the distribution of *Neptunea* can be seen in their species contents. Thus, *N. ventricosa heros*, *N. beringiana* var. *cordata*, *N. b.* var. *unicostata* and *N. communis* var. *borealis* (species of only the Boreal-Arctic group) are reported from Anadyr Bay. In Bristol Bay, in addition to the above species, *N. lyrata* and *N. aminata* occur. In the northeastern part of the Bay only Boreal-Arctic species were found, and in the southwestern part Boreal-Arctic and widely distributed Boreal and Boreal bathial species were found. *Neptunea ventricosa heros* and *N. beringiana* var. *costata* were the most abundant species in both bays. Catches in these regions can reach 100 kg/hour by sweeping with a 27.1 m trawl. In Karaginsky Bay, the main species (large accumulations are not recorded) is *N. laticostata ochotensis* (a north-Boreal species). *Neptunea lyrata* var. *phoenicea* (a widely distributed Boreal species) sometimes occurred. One-hour sweeping yielded 50 kg of these mollusks. Small accumulations of *Neptunea* occur in Norton Bay. *Neptunea* are represented here mostly by *N. ventricosa heros*, *N. communis* var. *borealis* and *N. beringiana* var. *cordata* (Boreal-Arctic species). However, there were cases when 1-hour sweeping failed to yield 0.5 kg of *Neptunea*.

Small accumulations of *Neptunea aminata* (a Boreal bathial species) were found off the edge of the continental slope in the central part of the Bering Sea. Catches here sometimes amounted to 40-50 kg from 1 sweeping. Such accumulations of *Neptunea* are not stable; observations conducted in the Bering Sea in 1973 did not confirm the previous year's data.

The regularity of the distribution of *Neptunea* in the Bering Sea with regard to Andriashev's zoogeographical barrier should be noted. North of this barrier are found only *Neptunea* belonging to the Boreal-Arctic group, while south of this barrier warmer water species together with Boreal-Arctic species are found. This suggests that Andriashev's zoogeographical barrier is a southern border of the Arctic in the Pacific.

Neptunea are of great interest for the fishing industry, but, in order to avoid an exhaustion of their reserves, it is necessary to continue studies on their biology. Special attention should be given to their feeding, possible methods of migration, and growth rates.

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SYSTEMATICS OF THE SUBFAMILY LAEVICARDIINAE KEEN 1936 (BIVALVIA: CARDIIDAE)[1]

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Abstract

In 1936, while preparing the revision of the family Cardiidae, A. Myra Keen found it necessary to single out a new subfamily, the Laevicardiinae, to include the following generic and subgeneric groups: *Laevicardium* Swainson 1840, *L. (Dinocardium)* Dall 1900, *L. (Fulvia)* Gray 1853, *Cerastoderma* Poli 1795, *Serripes* Gould 1841 and *Clinocardium* Keen 1936 (Keen, 1951, 1969). Kafanov (1974) recently subdivided the latter genus into 3 generic-group taxa: *Clinocardium* s.s., Keen 1936, *C. (Keenocardium)* Kafanov 1974 and *Ciliatocardium* Kafanov 1974. Also, the subfamily Laevicardiinae does not represent a natural group; *Cerastoderma* and *Clinocardium* s.l. have different centers of origin. *Cerastoderma* is linked with the Paleogene basins of the Eastern and Central Parathetys and the *Clinocardium* is linked with the North Japan-Sakhalin marine Paleogene province. Both of these taxa occupy their own adaptive zones and evolved in each case as the result of specific adaptive radiation processes and subsequent adaptive shifts. Their few similar morphological features are evidently due to the presence of characters inherited from some common ancient ancestor, which probably was some type of *Laevicardium* s.l. Referring *Cerastoderma* to its own individual subfamily is expedient, because the whole series of generically rich Neogene subfamilies of neolymnitic genesis, such as Lymnocardiinae Stoliczka 1870, Didacninae Eberzin 1962 (non Nordsieck 1969), Paradacninae Eberzin 1964, Hypaninae Starobogatov 1970 (pro Adacninae Vest 1875) and Prosodacninae Andreescu 1974, are directly connected with this genus and originated from some lagoon cardiid such as the modern *Cerastoderma glaucum* (Poiret 1789) (Eberzin, 1959, 1962, 1965; Starobogatov, 1970). By the same reason, it is correct to single out the independent family Lymnocardiidae, but only with the inclusion of *Cerastoderma* and related genera.

The genus *Serripes*, in spite of its peculiar features, is most closely related to *Clinocardium* s.l. and has common phylogenetic roots with it, as evidenced by the type of shell microstructure common to both (Popov, 1976).

Thus, the systematics of the subfamily Laevicardiinae *sensu* Keen may be represented as follows:

Family Lymnocardiidae Stoliczka 1870
  Subfamily Cerastodermatinae Nordsieck 1969
Family Cardiidae Lamarck 1809
  Subfamily Laevicardiinae Keen 1936
  Subfamily Clinocardiinae Kafanov subfam. nov. [1975]
    Tribe Clinocardiini Kafanov tr. nov. [1975]
      Genus *Clinocardium* Keen 1936 emend. Kafanov 1974
        Subgenus *Clinocardium* s.s.
        Subgenus *Fuscocardium* Oyama 1973
      Genus *Keenocardium* Kafanov 1974
      Genus *Ciliatocardium* Kafanov 1974
    Tribe Serripedini Kafanov tr. nov.
      Genus *Serripes* Gould 1841 (ex Beck, MS)
      Genus *Yagudinella* Kafanov gen. nov. [1975]

Diagnoses of new taxa are given below.

Clinocardiinae Kafanov subfam. nov. [1975]. Shell of average or large size, from oblong-elliptical to bevelled triangular; radial ribs 22-60, complanate-rounded, chevron-shaped or triangular in cross section; ribs psilate or having periostracal cilia arranged in longitudinal rows or covered with nodulous tubercles, but never with scales; if the external surface sculpture is reduced, then the traces of radial ribbing are seen on the back surface of the valves and more seldom on the front surfaces; on the right valve there are 2 cardinal, 2 anterior and 1 posterior lateral teeth; in the left valve there are also 2 cardinal, 1 anterior and 1 posterior lateral teeth, the latter more often being bifidate; the ligament is oblong, narrow and low. Upper Eocene(?), Lower Oligocene, Recent.

Clinocardiini Kafanov tr. nov. [1975]. Has the diagnosis of the subfamily, but the radial ribs are not reduced. Upper Eocene(?), Lower Oligocene, Recent.

[1] The date of publication for all new taxa established here is 1975 (Russian original).

Serripedini Kafanov tr. nov. [1975]. Radial ribs are very reduced or completely reduced, although they may be traced on the back and, more seldom, on the front valve surfaces; the hinge is reduced because of the cardinal teeth. Upper Oligocene, Recent.

Yagudinella Kafanov gen. nov. [1975]. Type species, *Cardium (Serripes) notabile* Sowerby 1915, Recent, Japan. Shell of average size or rather large, convex, bevelled, inequilateral, the front edge of each valve considerably narrower than the back edge; the back branch of the dorsal edge turns into the back edge at a well defined, obtuse angle; the back valve surface, as a rule, is with a visible bend; the valve tops are usually inclined forward, prosogyral; on the front and back valve surfaces are clear traces of radial ribbing; cardinal teeth reduced, but not completely. Middle Miocene to Recent. The genus is named in honor of the oldest laboratory assistant in the Mollusca Department of the Zoological Institute of the Academy of Sciences of the U. S. S. R., Saida I. Yagudina.

The following species are included in this genus: *Yagudinella notabilis* (Sowerby 1915) [=*Serripes notabilis nomurai* Otuka 1943, *fide* Noda 1962], *Y. makiyamai makiyamai* (Yokoyama 1928), *Y. makiyamai nigamiensis* (Noda 1962), *Y. shiobaraensis* (Noda 1962) and *Y. yokoyamai* (Otuka 1935).

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STRUCTURE AND HISTOPHYSIOLOGY OF THE CENTRAL NERVOUS SYSTEM OF *MIZUHOPECTEN YESSOENSIS* AND *CRENOMYTILUS GRAYANUS*

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Abstract

The central nervous system (CNS) of *Crenomytilus grayanus* and *Mizuhopecten yessoensis* has been studied by morphological, histochemical and electron microscope methods. The ganglia of *Mizuhopecten* and *Crenomytilus* are formed in a single plan which is characteristic of most Protostomia. They are enveloped by connective tissue underlain by nervous cells forming a crustal layer. The central part of the ganglion is made up of neuropiles, with a small number of fine and medium sized neurons.

Interneuronic relations in the nervous system of *Mizuhopecten* and *Crenomytilus* are restricted mainly to the neuropile. Histochemical studies show that synapses have a cholinergic and adrenergic nature. Monoamines are found also in singular neurons, which do not form localized congestions. Nervous cells of ganglia of *Mizuhopecten* and *Crenomytilus* contain neurosecretoric inclusions. In addition to promoting and transmitting nervous impulses, most (possibly all) neurons are capable of peptidergic secretion, which testifies to a lower level of neuron specialization. Considerable fluctuations of activity of the neurosecretory system have been observed during the year, which can be correlated with sexual activity of the animals.

Besides similarities, there are also some differences in structure and histophysiology of the nervous system of *Mizuhopecten* and *Crenomytilus*. The CNS of *Crenomytilus* consists of 3 pairs of ganglia, connected by long connectives. The visceral ganglia of *Crenomytilus* are joined into a single ganglion; the cerebropleural and pedal ganglia are closely adjacent and situated in the cerebral part of the body. The ganglia of *Mizuhopecten* contain larger neurons; in the crust layer they are regularly arranged. Cholinesterase is found in the neuropiles of *Mizuhopecten* ganglia. The arrangement of cholinesterase in places of localization of numerous synaptic contacts increases considerably the functional effectiveness of the nervous system (Sakharov & Turpajev, 1968). The differences mentioned above are evidently related to the greater activity of *Mizuhopecten*.

Two periods of increase and decrease of neurosecretory activity are seen in the nervous system of *Mizuhopecten* during the year, and at least 4 are seen in *Crenomytilus*. It is known that neurosecretory substances in invertebrates take part in the regulation of sexual and other physiological functions. Therefore, common activities of the mollusks studied coincide with the high level of secretory activity of the neurons. The differences in secretory activity of *Mizuhopecten* and *Crenomytilus* are dependent on ecology and especially on thermal conditions of the environment. *Crenomytilus grayanus* is a Lower Boreal species, penetrating into subtropical waters (Golikov & Scarlato, 1967). The thermal ranges of its general and sexual activities are rather wide (Dziuba, 1971). *Mizuhopecten yessoensis* is a species of more temperate waters; it ceases spawning when the water temperature reaches 18°C. As temperature increases further, the level of physiological processes decreases significantly, resulting in extremely low secretory activity of the neurons during the summer period.

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THE RESPONSE OF NEUROSECRETORY CELLS OF *MYTILUS EDULIS* TO LOW SALINITY

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Abstract

The neuroendocrine system of *Mytilus edulis* Linnaeus is represented by a relatively great number of separate groups of neurosecretory cells (NSC) located in the ganglia of the central nervous system. The cerebral ganglion contains the greatest number of NSC. Several groups of NSC can be arranged according to their size and location. Most abundant are small pyriform cells 9 x 18 mkm in size. Cells of this group are situated in the periphery of the ganglion, very close to each other. Small NSC differ in having vacuoles in the cytoplasm, which usually appear in the very periphery of the cell. Vacuoles increase in size and number and gradually spread throughout the cytoplasm. The nuclei of such cells shift to the axon pole and assume an irregular shape. All of these processes reflect a particular stage of the neurosecretory cycle. Neurosecretory material is secreted along the axons, which branch into the central neurophile zone of the ganglion. The other group is formed by large NSC, which are not so abundant as small ones. These cells are arranged in small accumulations (2-3 cells), but sometimes single cells occur. The average size of the cells of this group is 12 x 40 microns. The cell body very smoothly passes into the axon, and stretches for a small distance. Large NSC are closer to the ganglion centre than are small ones. In the cerebral ganglion of *Mytilus*, there is a small number of NSC belonging to a 3rd group. They are located closer to connectives and their axons stretch to the periphery of the ganglion, where they end, forming small terminal enlargements. The cells of this group are, on the average, 9.5 x 18 microns in size. The placement of *Mytilus* into dilute sea water results in some changes in NSC associated with the neurosecretion process. The fresher the water, the more intensive is the neurosecretion. At low salinity, the process of neurosecretion from the NSC has some peculiarities. The above groups of NSC respond to salinity changes in different ways. The most sensitive are the axons ending in the periphery of the ganglion, followed by small NSC and, last, less sensitive are large NSC situated close to the neuropile. Also, in some NSC (a group of small cells) there are dilations on the axon terminations. There are a small number of large and small NSC in the visceral and pedal ganglia. A neurosecretion from NSC takes place from these ganglia at low salinity, but the process is less intensive than in the cerebral ganglion. The neurosecretory system of *Mytilus* responds differently to a decrease in salinity, depending on the degree of the salinity changes. These mollusks are eurybiontic and under natural conditions undergo considerable fluctuations due to environmental factors, corresponding to natural fluctuations in their habitat. In this case, a neurohormonal regulation is accomplished due to a regular neurosecretory cycle of the NSC. In cases when changes in the factor (or factors) are considerable, but in the ranges of these changes the animals survive, the NSC at first sharply change their functional activity (neurosecretion and formation of dilated axon terminations). After that, a new rhythm of the secretory cycle is formed in the NSC, corresponding to changed environmental conditions. It should be noted that the intensification of the affecting factor does not cause a dilation of the axon terminations filled with products of neurosecretion which are associated with a mobilization of neurohormonal reserves. And finally, when environmental changes are so great that the animals cannot stand them, then degeneration of elements of their neurosecretory system begins.

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SPERMATOGENESIS IN *CRENOMYTILUS GRAYANUS* AND *MIZUHOPECTEN YESSOENSIS*

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Abstract

Seasonal morphological modifications in testes of 2 species of bivalved molluscs, *Crenomytilus grayanus* (Dunker) and *Mizuhopecten yessoensis* (Jay), have been studied. For this purpose, animals from the Ussuri Gulf (Sea of Japan) were caught at least twice a month during 1971-73. The gonads of *Crenomytilus* and *Mizuhopecten* represent an increased internal folia of the coelom and consist of follicles and efferent ducts, separated from each other by connective tissue tubercles. Spermatogonia occur on a basal membrane and, as they differentiate, move towards the center of the follicles, where they are transformed into spermatozoa. Before spawning (which for *Crenomytilus* and *Mizuhopecten* takes place at different times), follicles contain mainly mature sex cells. Due to the dependence of general and sexual activity of molluscs upon environmental temperature, the morphology of gonads changes considerably at different seasons. These changes are repeated regularly from one spawning to another and, taken as a whole, represent a sexual cycle consisting of several stages, which are characterized by the presence of cells of certain degrees of maturity.

The gonad goes into a state of rest after spawning. At this time, the gonad has its minimum size, is folded, and has a nonturgescent wall; small follicles are free of sex cells. This is the 1st stage of the sex cycle, and for *Mizuhopecten* lasts from the middle of July until the middle of September, and for *Crenomytilus* occurs during the whole 1st month of autumn.

Gametogenesis begins with abundant formation of spermatogonia (2nd stage), taking place for *Mizuhopecten* during October-December, and for *Crenomytilus* during the whole reproductive cycle. Besides spermatogonia in the gonad, a small number of spermatocytes is differentiated during this stage.

Active gametogenesis is characteristic of the 3rd stage. The gonads are dense and have increased in size. The follicles reach their maximum size. The gonad of *Crenomytilus* contains cells of different degrees of maturity, but primary and secondary spermatocytes predominate. In December, the gonad of *Mizuhopecten* contains mainly primary spermatocytes, and secondary spermatocytes in January and the following months. This stage for *Crenomytilus* lasts until May; for *Mizuhopecten* until the middle of April.

At the 4th (pre-spawning) stage, abundant formation of spermatids takes place in the gonads of *Crenomytilus* and *Mizuhopecten*, part of which are differentiated into spermatozoa. This stage for *Crenomytilus* lasts from May until June; for *Mizuhopecten* it lasts from the middle of April until May.

Spawning is the 5th stage. The gonad reaches its maximum size just before spawning. The follicles contain mainly spermatozoa, the output of which for both *Mizuhopecten* and *Crenomytilus* begins in May, but terminates at different times – for *Mizuhopecten* in June and for *Crenomytilus* at the very beginning of September. Spawning of *Crenomytilus* coincides with the pre-spawning stage during a considerable part of the year due to the portional character of the sex cells in reaching maturity. The development of the male sex gland appears to be correlated with cyclic changes in the female gonad. Males have spermatozoa at the outset of spawning, whereas the female gonad contains primary ovocytes.

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ECOLOGICAL EVOLUTION IN CEPHALOPODS

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Abstract

There are 5 main ecological groups (life forms, "Lebensformen") among Recent cephalopods: a nektonic, a benthic, a nektopelagic, a benthopelagic (near-bottom pelagic), and a planktonic form. There are also some transitional types. The evolution of cephalopods from the early Cambrian was determined by a most important aromorphosis: the development of a strong buoyancy mechanism (shell partially filled

by a light liquid). This mechanism permitted the bottom-dwelling ancestors of cephalopods to migrate into a new adaptive zone and to produce a benthopelagic lifestyle, which was an initial condition for the derivation of this class and was represented by Orthoceratida, Nautilida, etc., and among Recent forms only by *Nautilus* and Cirroteuthidae.

The 2nd aromorphosis was manifested in the appearance of the ammonoids: a lightening of the shell, oligomerization of the radula, appearance of the ink sac, and transition from direct development to development with a pelagic larval stage. This marked the beginning of the transition from the benthopelagic life form to the nektobenthic form, and also to the planktonic and benthic forms. But ammonoids got off early on the path of specialization.

The 3rd aromorphosis manifested in the appearance of the belemnites: the removal of the internal shell and the appearance of a muscular mantle and a mantle-funnel propulsor organ. In this way the nektobenthic life form appeared. The formation of Recent cephalopod types was the result of the 4th aromorphosis: rejection of the passive buoyancy mechanism in squids and octopuses or its radical change in sepiolids, but also with its final rejection on the next evolutionary phase (in sepiolids). The progressive evolution of Recent cephalopods follows 3 main lines, corresponding to nektonic, nektobenthic, and benthic life forms.

Recent nektonic species are present only in the Oegopsida (mainly at the beginning and in the middle of their evolutionary line) and in one of the sepiolid genera, *Heteroteuthis*. The nektonic life form is represented both by nerito-oceanic species, connected with the bottom (mainly with the slope) in the time of spawning, and by true oceanic forms. The former group is more primitive than the 2nd one. Big nektonic oceanic species are found only in 4 families and 6 genera of squids, and inhabit only 2 rather strictly defined ecological niches. It may be supposed that this type appeared rather late in the course of evolution and any outburst of taxonomic radiation is not yet evident.

Nektobenthic cephalopods belong to 2 evolutionary lines: neritic squids (Myopsida) and cuttlefishes (Sepiina). This life form has appeared independently and parallelly in both lines. In sepiids, "a new improved model" of strong buoyancy mechanism evolved; in other groups this mechanism has been lost. In both lines in the most advanced groups, tendencies to weaken their ties with the bottom and to approach a nektonic mode of life can be observed (*Doryteuthis, Alloteuthis, Uroteuthis* and *Heteroteuthis*), whereas a strengthening of ties with the bottom can be seen in aberrant specialized groups inhabiting the upper sublittoral zone (*Sepioteuthis, Pickfordiateuthis* and *Idiosepius*). But true oceanic nektonic forms have not appeared in both lines, as neither neritic squids nor cuttlefishes were capable of adapting themselves to spawning in midwater.

True benthic species are found only among octopuses of the family Octopodidae. Their benthic mode of life evidently evolved from the benthopelagic mode of life of cirrate octopuses through forms ecologically similar to *Palaeoctopus*. Recent Cirrata are deep-water and very specialized organisms, but even in their evolution the strengthening of their ties to the bottom can be observed (from Cirroteuthidae to Opisthoteuthidae). The Octopodidae have reached perfection in the adaptation to the benthic mode of life. Evolutionary tendencies in this family are restricted to idioadaptations only. Most primitive octopuses are shallow-water or eurybathic animals; the most advanced ones are deep-water inhabitants.

Every one of the 4 main ecological groups (benthopelagic, nektobenthic, nektonic and benthic) repeatedly gave origin to specialized semiplanktonic and planktonic forms which arose independently and convergently. Such forms are known among cuttlefishes (*Spirula*), squids (in 16 oegopsid families, of which 5 include only planktonic species), *Vampyromorpha* and octopuses (4 independent lines: *Cirrothauma* among Cirrata, 2 of the 3 bolitaenoid families, 1 of the 2 octopodoid families and 3 of the 4 argonautoid families). The adaptation to the planktonic mode of life was connected with solving 2 evolutionary problems: maintaining the neutral buoyancy with minimal energetic expenditures, and transition from bottom spawning (ancestral to cephalopods) to spawning in midwater. The passage to the planktonic form was the main path of specialization in squids and octopuses. Only in 1 evolutionary line of squids – in the so-called "longtailed Taoniinae" (of the most specialized family Cranchiidae) – can an attempt to return to a nektonic life form be observed. The process of transition from nektonic to planktonic can be well observed in Gonatidae and Onychoteuthidae, and transition from benthic to planktonic in the Argonautoidea. Nearly all planktonic and semiplanktonic cephalopods are deep-water inhabitants; the only epipelagic planktonic cephalopods are *Tremoctopus, Ocythoe* and *Argonauta*, and their adaptations are mostly unique. The effective conquest of the deeps by cephalopods became possible only after they rejected their external shell and worked out a different buoyancy mechanism.

Evolutionary progress and specialization in cephalopods are connected not with a widening or narrowing of the ancestral adaptive zone, but with the transition into another zone. The differences between aromorphic and telemorphic cephalopod groups can be explained only by the differences in overall height of organization and vital energy. Taxonomic radiation is a typical process in all forms except persisting ancient groups, but in the evolutionarily advanced groups the number of genera and ecological types is less than in specialized groups. Evolutionarily advanced groups of cephalopods mainly inhabit the shelf and epipelagic zone; specialized groups mainly inhabit the depths of the oceans. The general progressive

evolution of cephalopods on the tropical shelves is produced in a cruel struggle with competitors, mainly fishes. The joint evolution (co-evolution) of cephalopods and fishes has taken place from the late Palaeozoic up to Recent times, and many times first one then another group forced out its competitors.

Each stage in the evolution was adaptive, so that differences between arogenesis on the one hand and allogenesis and telegenesis on the other cannot be explained using the routine scheme of microevolutionary processes. Orthogenesis must be connected with the process of climatic orthoselection or with the epigenetic limitations, and thus also cannot guarantee a long maintenance of the same direction of selection (to aromorphosis). A hypothesis is proposed that the main motivating power of progressive evolution consists in the co-evolution of 2 (or more) competing groups in an active struggle for predominance in the most suitable living zone. The selection in such a process is directed not only to the development of particular adaptations, but first of all to the overall increase in structural organization and vital energy. This can guarantee a rapid developing of "evolutionary novelties" in both co-evolving groups. The victory of one of these competing groups involves the loss of any impetus to further evolutionary progress in the conqueror group, and this group might then retire to the way of specialization or hypermorphosis. The group that suffered defeat in the competitive struggle can retire into such an adaptive zone where the competition is weak and active predators do not play a significant role (e.g., into the depths), and there give rise to an outburst of taxonomic radiation. Aromorphosis, allomorphosis, and telemorphosis are 3 successive stages of the evolution of each great line, but the 1st stages of this process proceed, as a rule, in highly productive but ecologically unstable environments, in relatively simple, less mature ecosystems, and the last stages (in conditions of ecological stability) in complex, polymixtous ecosystems approaching maturity, where intraspecific competition is more intense than interspecific competition, and the selection favors the narrowing of niches.

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COMPARISON OF CEPHALOPOD FAUNAS ALONG THE COASTS OF CENTRAL AMERICA

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Abstract

Marine faunas of the American Mediterranean Sea (AMS: Caribbean, Gulf of Mexico and adjacent waters) and the eastern tropical Pacific (ETP) have many genera in common, which are not found in other areas, and some sibling species. The degree of similarity between faunas of AMS and ETP is rather high in shallow waters and rapidly diminishes with increasing depth. The degree of similarity is very different in various groups of marine organisms, even from the same depth. In some groups closely related forms can be found even in the abyss. These differences are probably connected with differences in the rate of evolution in various groups.

The areas now included in AMS were connected with the Pacific Ocean for the first time in the Jurassic. The last connection between the 2 regions was broken in the shelf areas in the Lower or early Middle Pliocene. So the deep-water faunas of AMS and ETP have been isolated from each other for at least 10-15 million years, and the upper sublittoral faunas for at least 4-5 million years.

A full list of cephalopods was compiled to use for the comparison of the faunas along both coasts of Central America: in the AMS from Cape Canaveral to the mouth of the Orinoco, including the Bahamas and the waters from the outer side of the Antillean arch (100 species in all) and the ETP from extreme southern California to middle Chile (110 species). (The full lists are published in: *Tr. Inst. Okeanol. Akad. Nauk. SSSR*, 1975, 100: 274-280, 285-286.) Non-tropical species (subtropical, boreal, notalian), entering these areas from the north and the south, comprise 9% of the total number of species in AMS and 25% in ETP. The number of benthic (B), nektobenthic (NB), benthopelagic (BP), pelagic neritooceanic (NO) and pelagic oceanic (O) species is as follows. It can be seen that the number of benthic and pelagic oceanic species is of the same order of magnitude, but the fauna of nektobenthic and neritooceanic species in ETP is much depauperized.

	B	NB	BP	NO	O	Total
AMS - All species	15	13	4	15	53	100
Tropical only	14	12	4	13	48	91
ETP - All species	25	4	3	3	75	110
Tropical only	18	3	3	1	58	83

Twenty-six to 28 species are common for AMS and ETP, which equals about ¼ of all species in each area. One of these (*Chiroteuthis veranyi*) enters the ETP from the south; all the others are world-wide or circumtropical species. Twenty-four to 26 species are oceanic, 1 is nerito-oceanic, and 1 is benthic, but has a prolonged pelagic larval stage. Several oceanic species are represented in AMS and ETP by different subspecies or forms. Nearly all circumtropical species which are common to both AMS and ETP are also found in Australo-Indonesian seas, and about 60% of them are reported off South Africa, so a potential gene flow between Atlantic and Pacific populations may exist via the Indian Ocean.

In 3 widely distributed genera there are pairs of closely related species inhabiting, correspondingly, ETP and AMS: *Lolliguncula panamensis – L. brevis; Octopus chierchiae – O. zonatus; O. oculifer – O. hummelincki; O. bimaculatus – O. maja; O. digueti – O. joubini;* and *Benthoctopus* sp. aff. *januarii – B. januarii.* It is probable that these species diverged from common ancestors after the isolation of ETP from AMS, but this can be definitely affirmed only for the pair *O. chierchiae – O. zonatus,* as other pairs have related forms in the seas formerly connected with the Tethys Sea. All of these pairs inhabit the upper sublittoral zone, except *Bathypolypus,* which are bathyal. The abyssal fauna is represented in ETP and AMS by some unnumerous, insufficiently known and partly undescribed species of the world-wide genera *Grimpoteuthis* and *Cirroteuthis,* and by unidentified Bathypolypodinae; it is impossible to say anything definite about their relationships.

The monotypic family Pickfordiateuthidae is an endemic of AMS, the genera *Nectoteuthis, Selenoteuthis* and *Tetracheledone* are endemics of the tropical western Atlantic, including AMS. Five genera are endemics of ETP: *Loliolopsis, Dosidicus, Drechselia, Froekenia* (a doubtful genus) and *Euaxoctopus.* Of non-endemic tropical genera found in ETP, only *Amphitretus* is definitely absent in AMS; but of the non-endemic genera found in AMS, many are totally absent in ETP: e.g., 3 families (Spirulidae, and Lycoteuthidae) represented in AMS by 9 genera and 12 species, the genera *Sepioteuthis, Doryteuthis, Ornithoteuthis, Pholidoteuthis, Chiroteuthoides, Egea, Sandalops, Scaeurgus, Pteroctopus, Danoctopus* and some others.

The noticeable depauperization of the fauna of nektobenthic and nerito-oceanic cephalopods in ETP contrasts with the high diversity of sublittoral bottom octopuses: there are 20 species in ETP, among which 13 are tropical endemics, while in AMS there are only 9, among which only 5 are endemics. The depauperization of the fauna of nektobenthic and nerito-oceanic cephalopods in ETP may be accounted for by the supposition that the active evolution of these groups began in AMS only after the connections between AMS and ETP were broken. However, it seems to be more likely that the tropical fauna of ETP was formerly rich, but has been decimated during the Pleistocene due to changes in oceanic circulation, particularly under the influence of the widening and the rapprochement of upwelling areas now located off California and Peru. These changes could have had a particularly strong influence on the near-bottom waters in the lower sublittoral and upper bathyal zones, and a minor influence on the inner shelf, where the non-migrating bottom species could have found refuge.

The existence of a number of endemic genera and species and the small number of sibling species pairs in ETP and AMS show that the evolution of sublittoral, bathyal and nerito-oceanic cephalopods proceeded at a sufficiently high rate to have eliminated almost all evidence of past contacts between the areas of ETP and AMS for some millions of years. Also, oceanic cephalopods have enough possibilities for dispersing, and so among them evidence of previous contacts are not now detectable.

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EVOLUTION OF SQUIDS OF THE FAMILY HISTIOTEUTHIDAE IN RELATION TO PECULIARITIES OF VISION

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Abstract

Due to an asymmetrical development of their eyes, squids of the family Histioteuthidae are a unique phenomenon among cephalopods. Their left eye is nearly twice as large as the right eye. In regard to the adaptive role of such unusual differences in eye structure, there are diametrically opposed opinions.

According to Voss (1967) the large eye functions in poor illumination at great depths, while the small one is destined for vision in surface waters. Investigating the absorption properties of the crystalline lens in the Histioteuthidae, Denton & Warren (1968) came to the conclusion that the large eye is adapted for living near the sea surface, while the small eye is adapted for less illuminated abyssal waters.

Our knowledge of the behavior, mode and conditions of life of these squids is not enough to interpret the ecological reason for such an asymmetry. It is known that they are inhabitants of epi-, meso- and bathypelagic regions to a depth of 2000-4000 m, where they are quite abundant and are one of the main components of the food of sperm whales. Larvae of the squids occur most often near the surface. The squids are not very mobile and resemble Rhizostoma by their disproportionately large heads and long thin palps connected with a membrane.

An analysis of optical characteristics of the eyes reveals considerable differences between them. The absence of the yellow pigment or groups of pigments filtrating the ultraviolet rays from the external layers of the small crystalline lens makes the crystalline lens of the small eye more transparent. Also, the crystalline lens of the small eye is more short-focal: the focal distance of the small eye lens is about 1.5 times less. Due to a difference in size of the eyes, the light intensity of the lens is also different: the lens of the small eye passes twice as much energy to the focal plane than does the lens of the large eye. In addition, at the same position of the crystalline lens against the retina, the focal plane of the small eye is about 10 times closer than that of the large eye.

An analysis of anatomical and physiological properties shows that the eyes differ in the structure and area of the retina, the volume of conducting pathways and the volume of the central compartment for "interpreting" the optical information – the optical ganglia. The absolute sizes of rhabdomes in the retina of the large eye of *Histioteuthis bonnellii* are smaller than in the retina of the small eye, and correspondingly their density is 1.3-1.4 times more than that of the rhabdomes of the small eye. The retina area of the large eye is 1.5-2.0 times greater. Correspondingly, the volume of conducting pathways and optical ganglia of the large eye is 1.5-2.0 times greater than that of the small eye.

The adaptive sense of these differences consists in the following. The life of squids in differently illuminated water layers suggests a qualitative and quantitative change of optically perceptible information. Under conditions of complete darkness (at depths greater than 700-1000 m) the single source of light is bioluminescence. Due to this, things that are optically perceived are either luminous objects or objects which are near the squid and are illuminated with a reflected light radiated by the squid's photophores. In the Histioteuthidae, the asymmetry affects the photophores also. Around the small right eye there is a ring of well developed, closely situated, large photophores, while photophores around the large eye are far apart and some of them are rudimentary or even atrophied. Recognition of luminous objects at depths lacking light depends, in general, on the intensity of luminescence and on the threshold sensitivity of the retina. It is clear that under such conditions the eye with more intensive optics, i.e., the small eye, has advantages. The more intensive optics of the small eye and the greater transparency of its crystalline lens, in combination with illumination created by well developed photophores, favor the adaptation of the small eye to great depths.

Due to a difference in the absolute size of the eyes, the representation of the objects on the retina of the large eye will occupy a great area. As far as the density of the receptor elements in the retina of both eyes is unequal and the difference in the total number of the receptor elements in the retina of both eyes is accompanied by differences in the volume of conducting pathways of the optical lobes (a summation of the information does not take place), the resolving ability of the large eye will be higher. In addition, the keenness of vision of the left eye is favored by yellow pigments of the external layers of the big crystalline lens, which, as is known (Orlov, 1974), remove the chromatic aberration and blue haze of diffusion, thus intensifying the contrast of the object against the background. The greater differentiative and distant ability of the large eye suggests that it is better adapted to functioning in illuminated layers of water.

As a result, the conclusion can be drawn that the small eye is more specialized as compared to the large eye, which in its development is close to the eye of other cephalopods and fishes. Thus, the evolu-

tion of the squids of the family Histioteuthidae was directed towards adaptation to life in darkness, which was accompanied by structural changes in the optic system, whose important role has been preserved within the evolutionary history of this group.

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PECULIARITIES OF THE SEASONAL DISTRIBUTION OF THE NORTH AMERICAN SQUID *LOLIGO PEALEI* (LESUEUR 1821)

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Abstract

In the waters of the western Atlantic, the North American squid *Loligo pealei* is distributed from the peninsula of Nova Scotia in the north to Venezuela in the south. Our researches embraced the shelf area from Cape Hatteras to Nova Scotia. Within the borders of this range, *L. pealei* is not evenly distributed. In the south – in the Caribbean Sea and the Gulf of Mexico – it is less numerous than on the American shelf to the north of Florida. This squid was checked in great numbers in the slope and shelf waters to the north, up to Cape Hatteras.

The formation of concentrations of squids depends to a great extent on the peculiarities of the hydrological regime in the area. The circulation of water masses along the eastern coasts of North America depends on the interaction of the Cabot Stream and Gulf Stream waters. Off the shelf, a large zone extends where northern waters mix with waters of tropical origin. The densest concentrations of squids are connected with frontal zones with strong temperature gradients. Such concentrations near the junction sites of different water masses are located mostly along the warm water.

The North American squid lives at depths from 2 to 450 m, mostly from 30 to 250 m. In connection with the seasonal bathic migrations, the optimal depths for squid change in different months: December to April – 100-250 m; July to August – up to 75 m; September to November and in May – 50-100 m. The bathymetric distribution of different age groups of squid differs: the young usually keep nearer to the coasts, so the average size of the squid caught increases with increasing depths. An analysis of the seasonal distribution of the age groups of squid makes it possible to present the pattern of their seasonal migrations in the following way. In April-May, the squid migrate from the open shelf into the coastal waters at depths of 20-50 m with temperatures of 7-9°C. From June to September (at temperatures of 10-18°C) reproduction and quick growth of the fry takes place here. In this period, the reproductive part of the squid's range coincides with the feeding part of the range. In September and until the beginning of November, a displacement of the young squid and maturing ones to the waters close to the slope (50-100 m depth, temperatures of 9-14°C) takes place, and active feeding continues. The autumn migration takes place usually in the feeding part of the squid's range. During December to March, further growth and maturation of gonads take place in the waters of the slope (100-250 m depth, sometimes deeper, temperatures of 9-12°C). In the spring, mature squids migrate to the shoals for spawning, and those not yet mature migrate to the shelf, where fattening takes place.

The northern border of the squid range undergoes considerable seasonal displacement: in summer this squid may be found up to 45°30′N, and in winter only to 40°50′N. Such a difference can be explained by the great winter cooling of waters in this area. The distance between the summer and winter limits of distribution of squid to the north is about 800 km.

In hydrologically warm years, the spring migration of squid to the shelf and to the north begins sooner than in cold years. Squid reach the extreme points of their range in the north, and make the return migration to the slope waters later in autumn. In such years, the feeding part of the squid's range widens considerably (embracing nearly the whole coastal area of the Gulf of Maine), the periods of reproduction and fattening lengthen, and it is possible that this is one of the reasons for the great fluctuations in numbers of squid in some years in the northern part of the range.

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DISTRIBUTION OF DEEP SEA CEPHALOPODS IN THE SOUTH ATLANTIC AND ADJACENT WATERS (MAINLY ANALYSES OF SPERM WHALES FEEDING)

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Abstract

Meso- and bathypelagic cephalopods of the southern Atlantic and adjacent part of the Pacific sector of the Antarctic (PsA) are nearly unknown. So the collection of cephalopods from the stomachs of sperm whales taken during 3 cruises of the Antarctic whaling factory "Yury Dolgoruky" (November to April, 1970-73) is of interest. The material was collected from 189 stations, averaging 2 samples per station. In the southwestern Atlantic (SWA) they were collected at 110 stations, in the southeastern Atlantic (SEA) from 14 stations, in the Atlantic sector of the Antarctic (AsA) from 42 stations, and in the PsA from 23 stations. The area of investigation extended from 28°30′ S to 68°20′ S and from 10° E to 130° W.

The list of cephalopods found contains 26 species from 14 families and 18 genera. Most species of squids (16) were common in the sperm whales' food, at least at some places.

In the area of SEA (30-43° S), big squids (*Taningia danae* and *Moroteuthis robsoni*), the "scaled squid" (*Lepidoteuthis grimaldii*), the giant squid (*Architeuthis* sp.) and relatively small squids (*Histioteuthis dofleini, H. macrohista, H. reversa* and *H. eltaninae*) commonly occurred in the sperm whales' stomachs. Up to 80% of the food volume consisted of the remnants of big squids, but, by frequency of occurrence, histioteuthids dominated. The size (mantle length) of the big squids was 40-70 cm, for giant squid, it was 100-160 cm, and for histioteuthids it was 8-15 cm.

In the area of SWA (30-50° S), the food of sperm whales was more diverse than in SEA. As in SEA, the common species were *Taningia danae* (mantle length 20-105 cm, average 60 cm), *Architeuthis* (up to 160 cm, average 70 cm), *Moroteuthis robsoni* (40-50 cm), and *Lepidoteuthis* (up to 75 cm, but as a rule 30-40 cm). *Moroteuthis robsoni, L. grimaldii* and *T. danae* were common in the northern parts of the SWA (30-45° S). The most common in the southern part (45-50° S) was *Moroteuthis knipovitchi* (30-45 cm), less common there were *M. ingens* (maximal size 114 cm) and *Mesonychoteuthis hamiltoni*. The last 2 species were characteristic for Antarctic waters. Among the octopuses of this area, the deep water *Alloposus mollis* plays a great role in the feeding of sperm whales. The big octopuses weighed 10-15 kg. The southernmost record was made at 51°20′ S. This octopus is common in tropical and subtropical waters and its penetration so far to the south may be connected with the seizure of warm waters of the Brazilian Current by marginal waters of the circumpolar West Wind Drift. Less common was *Ancistrocheirus lesueuri*. It is distributed through all the area, but is concentrated in warmer subtropical waters of the northern part of SWA. Most frequent here are small squids of the genus *Histioteuthis: H. macrohista, H. atlantica, H. dofleini* and *Histioteuthis* spp. (the first 3 were more frequent).

In the area of AsA, the most common species in the feeding of sperm whales (in the order of importance) were: *Mesonychoteuthis hamiltoni, Moroteuthis ingens, M. knipovitchi* and *Architeuthis* sp. *Mesonychoteuthis* was the main food of male sperm whales, as females rarely enter cold waters. In AsA, 2 regions may be distinguished where these squids are particularly abundant: to the east of South Sandwich Islands (55-60° S, 20-25° W) and in the western part of the Scotia Sea (53-59° S, 45-55° W). The size distribution of these squids was rather uniform in the same area: mantle length 55-165 cm. Relatively small specimens (smaller than 1 m) can be distinguished from the larger ones by the color of their bodies and the form of their fins.

In the area of PsA, *Mesonychoteuthis* is also a dominant species in the food of sperm whales. Large specimens (130-180 cm) were found up to 68° S. *Moroteuthis ingens* and *Moroteuthis* sp. were found in lesser quantities. The remnants of giant squid (*Architeuthis*) were recorded up to 66° S. These inhabitants of subtropical waters reach high latitudes, probably because deep warm water masses intrude into these areas. Among rare species were *Onychoteuthis banksi* (SWA), *Tetronychoteuthis dussumieri* (SWA), *Ommastrephes bartrami* (SWA), *Todarodes angolensis* (SWA), *Pholidoteuthis* sp. (SEA, identification is doubtful because of the bad condition of the specimen), *Psychroteuthis glacialis* (AsA), *Cycloteuthis akimushkini* (SWA), *Chiroteuthis* sp. (SWA) and *Galiteuthis* sp. (AsA). One species of squid could not be identified even to its family.

In general, the meso- and bathypelagic cephalopods are absolutely predominant in the feeding of sperm whales in the southern Atlantic. Deep water fishes occurred occidentally, and in some regions amounted to about 5-10% of the food volume.

Most specimens of the more common species of squids in the stomachs were adult and mature, or approached maturity. It is possible that sperm whales feed on pre-spawning or spawning squid concentrations. The analysis of squid distribution shows that such concentrations are found, as a rule, in productive waters over the slope and underwater ridges of the southern Atlantic and around the Antarctic divergence.

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LIST OF SPECIES AND THE DISTRIBUTION OF OCEANIC SQUID LARVAE IN THE EASTERN ATLANTIC

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Abstract

From 2,600 samples collected by the expeditions of the Atlantic Research Institute of Fisheries and Oceanography from 1966 to 1974 throughout the area of 30° N to 37° S and from the western coast of Africa to 26° W by the qualitative (plankton) net (80 cm in diameter; 600 samples) and by the Juday net (37/50 cm in diameter; 2000 samples) up to a depth of 500 m, larvae were found in only 409 samples. The identified larvae belonged to 23 species of squids of the families Cranchiidae (25% of all samples), Euoploteuthidae (24%), Ommastrephidae (22%), Onychoteuthidae (13%), Brachioteuthidae (11%), Chiroteuthidae (2.4%), Ctenopterygidae (1%), Octopodoteuthidae (0.8%) and Histioteuthidae (0.8%). In the most abundant samples were members of *Cranchia scabra* (17%), *Ommastrephes pteropus* (17%), *Abraliopsis* sp. (14%), *Brachioteuthis riisei* (regions XI-XII) (11%), *Onychoteuthis banksi* (7%) and *Galiteuthis armata* (6%).

The character of the quantitative distribution of the squid larvae depends on the peculiarities of the circulation of the water mass in the area investigated. Their greatest accumulations are confined to the regions of intensive upwelling. This is a region of the equatorial divergence (from 6-5° S to 7-8° N) and regions of coastal upwellings off the coasts of northwestern and southwestern Africa. Larvae of *Brachioteuthis riisei* (regions XI-XII) were most abundant in the oceanic part of the northwestern coast of Africa (30-10° N); larvae of *Ommastrephes pteropus* (regions VII-VIII) occurred throughout the whole aquatoria southwards of 17° N; larvae of *Cranchia scabra* (regions I-II) occurred southwards of 20° N and larvae of *Onychoteuthis carribaea* (regions X-V) occurred throughout the whole aquatoria. The subequatorial region is characterized by a great species variety of larvae. The common species are *C. scabra, O. pteropus, Abraliopsis* sp., *Abralia veranyi* and *P. giardi.* Less abundant are *Onychoteuthis banksi, O. carribaea* and *Galiteuthis armata.*

Relatively constant abiotic conditions stipulate year-round spawning. However, the number of larvae of all species found in the samples increased noticeably from January to March. Only single occurrences of *Ommastrephes sicula* (region XI) and *Chiroteuthis veranyi* (region I) are reported from this region.

In the open part of the coast of southwestern Africa (10-37° S), larvae of *Brachioteuthis riisei* (regions X-XII), *Onychoteuthis banksi* (regions XI-XII) and *Galiteuthis armata* (region VIII) were most abundant. Single larvae of *Cranchia siculus* (regions VIII-XII), *Chiroteuthis veranyi* (region IX) and *Onychoteuthis bartrami* (36°45′3 S-10°48′0 W; 35°43′0 S-31°59′0 W) were recorded in June.

For some species, larvae of which were most abundant in the samples, the borders of the reproductive part of the area can be established: for *Cranchia scabra* from 20° N to 10° S (year-round spawning); for nearly all enoploteitids of the subequatorial region (year-round spawning); for *Ommastrephes pteropus,* year-round spawning in the subequatorial region and a mass summer spawning peak in the region of 17° N to 10° N; and for *Brachioteuthis riisei,* mass spawning in regions I and III.

Almost all larvae found belonged to oceanic squids. Over 80% belonged to epi-, meso- and bathypelagic species, and 13% belonged to bathyal species.

In general, squids inhabit the upper 100 m layer of water. An adaptation was observed of larvae of different species for definite horizons: larvae of *Brachioteuthis riisei* occurred in the surface layer; those of *Ommastrephes pteropus* at a depth of 25-50 m; those of Euoploteuthidae from 0 to 50 m and those of *Cranchia scabra* from 50 to 100 m. No squid larvae were found in the samples from depths of over 150 m.

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AN APPROACH TO THE CONSTRUCTION OF SEXUAL MATURITY SCALES OF OVARIES IN SQUIDS

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Abstract

Recently a construction of scales has been started for a definition of maturity stages of the gonads of squids on the basis of the methods applied for fishes and shrimps. However, the transference of these methods from fishes and shrimps to the squids requires a serious correction of scales due to different types of gonad development in fishes and shrimps on one hand and in squids on the other.

The gonad development in squid, in contrast to fishes and shrimps, is characterized by constant asynchronism. Due to this, one can find in gonads of pre-spawning individuals oocytes at all phases of pre- and vitellogenesis. Such type of development aims at a gradual extension of maturation of eggs and spawning. However, most, and very possibly all, squids are characterized by a simultaneous laying of the whole mass of eggs. So, the contradiction arises between the aim of gonad development and the character of spawning. But the contradiction is removed by the formation of voluminous oviducts. During the maturation process, the eggs migrate to the oviducts and are preserved there until spawning.

Such a complex mechanism for the preparation of spawning can be assumed to be an anabolism, as compared to the ancestral way of gonad development. Apparently, initially for cephalopods, the spawning was protracted with a one-by-one egg laying, as it is supposed to take place in *Nautilus*. A somewhat similar phenomenon is observed in *Sepiida*, which lay eggs one by one. However, they have a primitive mechanism of accumulation of eggs only in the genital coelom, prior to the complex process of the formation of the tertiary membrane and attachment of each egg to the substratum.

In squids, eggs are smaller than those of *Sepiida* and *Nautilus*, but the fecundity is higher. This entailed the impossibility of laying eggs singly and the necessity of having an accumulative organ. Most of the squids have a common tertiary membrane enveloping the whole clutch. It is excreted by the nidamental glands.

The continuous asynchronism of gonad development in coastal and near-bottom ancestors of Recent cephalopods arose as an adaptation to the decrease in energetic expenditures during maturation and laying of large eggs. The squids assimilating the water mass have acquired another adaptation: a compensatory accumulating mechanism. The preparation for spawning in squids proceeds in 2 stages: gonad maturation and accumulation of mature eggs in oviducts. When constructing a scale for a definition of gonad maturity, principles used for fishes and shrimps can be applied to a periodization of the 1st stage (Sakun & Butskaya, 1968; Burukovsky, 1970; Kuznetsov, 1972). The 5th stage of maturity corresponds to spawning in fishes and shrimps, and in squids points to the appearance of mature eggs in the oviducts, i.e., to the beginning of the 2nd stage. Correspondingly, this stage consists of several phases. Proceeding from this assumption, we can suggest the following scheme for sexual maturity scales, which, however, must be specified for every species of squid by a description of corresponding changes and weight ratios in the gonad and its "service" organs (rudimental and oviductal glands, oviducts).

1st stage: Most developed oocytes are at the 1st phase of protoplasmatic growth.

2nd stage: Most developed oocytes are at the 2nd phase of protoplasmatic growth ("simple follicle" phase).

3rd stage: Most developed oocytes are at the 1st phase of trophoplasmatic growth ("complex follicle" phase).

4th stage: Most developed oocytes are at the 2nd phase of trophoplasmatic growth ("nucleus, changes" phase).

5th stage: Most developed oocytes are at the 3rd phase of trophoplasmatic growth ("mature egg" phase). The gonad contains the residual bodies and oviduct eggs.

This stage completes the 1st stage of gonad maturation. Since during the 2nd stage no principle histological changes proceed in the gonad, the accumulation of eggs is designated by gradations in the ranges of stage 5: $5_1, 5_2, 5_3$, according to the number of mature eggs in the oviducts.

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THE HELMINTH FAUNA OF ATLANTIC SQUIDS OF THE FAMILY OMMASTREPHIDAE (CEPHALOPODA: OEGOPSIDA)

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Abstract

Squids of the Ommastrephidae are a most abundant and widely distributed group of cephalopods in the oceans. Mass representatives of this family from the Atlantic can be arranged into 3 ecological groups:

1. Far-neritic squids of the genera *Illex* and *Todaropsis*. These inhabit mainly near-bottom layers of the shelf and the upper part of the continental slope; they are never found in the open ocean. They are 28-32 cm in size, usually 10-20 cm. They feed, in general, on crustaceans (copepods, euphausiids, etc.) and on young and small species of fishes and squids.

2. Nerito-oceanic squids of the genus *Todarodes*. These are confined, as a rule, to a continental slope of the continents and islands, but they can also occur in the open ocean. They live near the bottom as well as in the whole water mass, and can reach 74 cm in size, but are usually 15-30 cm. They feed on different crustaceans, fishes (Beloniformes, Clupeidae, Myctophidae, etc.) and cephalopods.

3. Oceanic squids of the genus *Ommastrephes*. These are distributed throughout the whole open part of the Atlantic. Their life cycles take place in the open ocean, mainly in epipelagic regions. They reach 80 cm in size, but are usually 15-30 cm. Their food consists mainly of myctophids, Beloniformes, young of flying fishes (Exocoetidae), squids, crustaceans (euphausiids, copepods and amphypods in general) and many other invertebrates.

A study of the helminth fauna of ommastrephids has revealed a rather narrow range of parasites. There are, however, considerable differences in the species composition, extensity and intensity of invasion of the members of some ecological groups of squids, depending on their age, size and habitat.

Todaropsis eblanae is characterized by a distinct local variability in infection with helminths. In 647 squid from the coast of northwestern Africa, no parasites were found. At the same time, in 96 specimens of *T. eblanae* off southwestern Africa, 13.5% were infected with *Anisakis* sp. 1_1 (7.2%), *Phyllobothrium* sp. 1_2 (5.2%) and *Scolex pleuronectis* (2.8%). In addition, cases of *Dinobothrium* parasitism in *T. eblanae* are reported.

Seven-tenths of a percent of the squid *Illex coindeti* from the coast of northwestern Africa (in all, 1,880 specimens were examined) were infected. In this case, infection with nematodes (*Porrocaecum* sp. 1) was 0.3%, with cestodes (*Scolex pleuronectis*) was 0.4% and with *Nybelinia yamagutii* was 0.05%. Thirty-four squid from the Ireland shelf were examined; 32% of these were infected. Infection with *Porrocaecum* sp. was 3% and with *Phyllobothrium* sp. it was 32%. According to data from the literature, squids are parasitized by larvae of *Dinobothrium* sp. In 49% of 76 individuals of *Illex illecebrosus* examined from the Ireland shelf, only larvae of *Phyllobothrium* sp. were found. At the same time, the general extensity of infection of squids from the Nova Scotian shelf was 38.1% for 1,000 specimens. In these *Phyllobothrium* sp., *Dinobothrium* sp., *Scolex pleuronectis*, *Nybelinia* sp., *Contracaecum* sp. and *Anisakis* sp. 1_1 were found.

Infection of the nerito-oceanic squid *Todarodes sagittatus* from northwestern Africa with larvae of *Phyllobothrium* sp. was 0.4% (254 squid were examined). Cases of parasitism of *Nybelinia* sp. and *Phyllobothrium* sp. 1 (2 species) in *T. sagittatus* were recorded. Infection of *Todarodes angolensis* from southwestern Africa was 5.4% (74 squid were examined). *Anisakis* sp. 1_1 were found in 1.3% of the squid, *Porrocaecum* sp. in 1.3%, *Tentacularia coryphaenae* in 1.3% and *Phyllobothrium* sp. in 2.6%. Only squid larger than 25 cm were infected.

The oceanic squid *Ommastrephes bartrami* from the northern (53 specimens) and southern (42 specimens) Atlantic was studied. The species composition of the helminth fauna in both areas was very similar; there are only small differences in the extensity and intensity of infection (98% and 80%, respectively). Two types of larvae of *Porrocaecum* sp. were found – small ones encysted on the stomach (96% and 72%, respectively) and large ones from the mantle walls (50% and 28.5%, respectively); *Anisakis* sp. 1_2 – 19.2% and 6.1%; *Nybelinia lingualis* – 25% and 6.1%; *Tancula* – 5.7% and 19%; *Phyllobothrium* sp. 1_1 – 1.9% and 3.0%; and metacercariae of the family Didymozoidae (type *"Monilicaecum"*).

One thousand thirty-nine specimens of *Ommastrephes pteropus* from different parts of the tropical Atlantic were examined. The infection extensity was very high (94.9%); in some squid larger than 25 cm 100% infection was observed. Nematodes of *Porrocaecum* sp. 1 were found in 75% of the squid (small ones in 73.6%, large ones in 26.4% of the squid), *Anisakis* sp. 1_2 in 25.3% and larvae of *Phyllobothrium* sp. 1_1 in 28.8%. Most frequent were representatives of the family Tentaculariidae (84.8%). Among these were *Tentacularia coryphaenae* (37.3%) and members of the genus *Nybelinia* (77.2%). The genus *Nybelinia* was represented by the following species: *N. yamagutii*, *N. lingualis*, *N. lingualis* var. 1 and *Ny-*

belinia sp. In regard to the trematodes, metacercariae of didymozoids (type *Torticaecum*; 12.5%), *Hirudinella ventricosa* (1.05%) and a single mature didymozoid trematoda (0.09%) were found.

An analysis of the species composition of helminths from ommastrephids has revealed 2 helminthcoenoses, coastal and oceanic. The main coastal forms are *Anisakis* sp. 1_1, *Phyllobothrium* sp. 1_2, *Dinobothrium* sp. and *Scolex pleuronectis*. The main oceanic forms are *Tentacularia coryphaenae*, *Nybelinia yamagutii*, *Phyllobothrium* sp. 1_1, *Anisakis* sp. 1_2, *Porrocaecum* sp. and metacercariae of the Didymozoidae. Such distinct differences in the species composition of the above helminthcoenoses refer not only to ommastrephids, but are a reflection of coastal and oceanic biocoenoses existing in the ocean.

A great specific variety of the helminths, and rather high indices of extensity and intensity of infection in the oceanic ommastrephids, are stipulated by their high ecological valence, as compared to the coastal representatives of this family.

The intraspecies and local variability in squid infection depends on the presence or absence of masses of parasites of ommastrephids, definitive hosts of helminths, and lastly on the historically formed trophic relations of the squid in a given region.

All helminths found in ommastrephids possess a wide specificity, and use for the same developmental stages many species of teleost fishes as intermediate hosts. The ancestors of ommastrephids "conquered" recent ecological niches on account of this or that group of teleost fishes, and acquired their helminths. Thus, the helminth fauna of ommastrephids is secondary in character and consists of typical "fish" forms.

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STRUCTURE OF THE SHELL AND EVOLUTION OF ONTOGENESIS IN THE CEPHALOPODA

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Abstract

Unlike other molluscs, Recent cephalopods have no larval stages in their development. The shelled forms (e.g., *Nautilus*, *Sepia* and *Spirula*) have no morphological and structural differences in their embryonic and postembryonic skeletons (except in size and some allometric growth patterns). The embryonic shell seems to be secreted not only by the shell gland, but also by the mantle, the differentiation of which was identical to that of mature forms. The initiation of the secretion of the embryonic shell has been shifted to comparatively later stages of embryonic development. The fossil cephalopods, which were connected with the phyletic branch which evolved into the Recent Tetrabranchia, have the embryonic shell structure principally like that of Recent *Nautilus*. Thus, direct development with comparatively late embryonic formation of skeleton is an early evolutionary acquirement, and it may be the primary type of ontogenesis in this branch. There are great structural differences in the initial parts of the shell of fossil cephalopods which are related to the ancestors of the Recent Dibranchia. These differences are, for example, a known morphological and structural feature of the 1st whorl of ammonids and the initial part of belemnites', orthocerids' and bacteritids' shells.

There are opposite views on ammonid development, i.e., from a direct one to development with several larval stages and metamorphosis. These differences are caused by a different interpretation of the boundary between embryonic and postembryonic parts of the shell. Three possible variants of the place of this boundary have been presented: at the end of the protoconch (Erben, 1964, and others); at the end of the 1st whorl, excluding the primary ("nepionic") constriction (Drushitz, 1958, and others); and at the end of the 1st whorl, including the primary constriction (Ivanov, 1971; Kulicki, 1974).

The principal problem lies not in the position of the embryonic shell boundary, but in the explanation of the existing structural reconstructions. In the initial part of the ammonid shell, it is possible to distinguish 4 morphologically and structurally different regions, which correspond to 4 stages of early ontogenesis: 1) protoconch formation, 2) formation of the 1st whorl, 3) primary constriction formation, and 4) formation of the 2nd and the following whorls. The structural reconstructions occur between the 2nd and the 3rd, and the 3rd and 4th stages.

Thus, the existence of structural changes shows that physiological mechanisms responsible for secreting the shell have undergone changes. Structural monotony of the protoconch and 1st whorl layers shows their secretion to be produced not by differentiated epithelium but rather by the shell gland (or by the primary mantle rollet as in the case of the veliger). The existence of nacreous layers in the primary constriction and in the shell wall of the following whorls testifies to the appearance of the mantle and to

its differentiation as well, as in the mature animal.

Thus, the start of ammonid shell formation occurs comparatively early, before mantle formation and differentiation, and before formation of the main internal organs of the mature individual type.

The hypothesis of larval development is more preferable than that of direct development. The stages of metamorphosis easily come into harmony with structural reconstruction (forming of the primary constriction). The protoconch-bearing initial parts of bacteritids and orthocerids have a similar construction. As was supposed formerly (Shimansky, 1962, and others), the development of the latter groups proceeds with "incomplete metamorphosis" and with a veliger-like larva. This larva was not a true veliger, because its planktonic behavior was warranted by a hydrostatic apparatus of the shell, but not by the velum.

Complex structural changes take place in early stages of the belemnite skeleton (Barskov, 1974). Belemnites had early deposition of the shell; their larvae apparently had an internal shell and so they can hardly be compared with veligers.

I propose the following scheme for the evolution of the cephalopod ontogenesis. The primary cephalopod larva (protocerella, non-planktonic) had a large conic shell with an apical opening (as Starobogatov postulated in 1974 for the larvae of molluscs with a dorsal visceral sac), no more than 1 chamber and no separated siphonal division. This construction resembled *Nanno* (Endocerida) and *Kochoceras* (Actinocerida). During the succeeding evolutionary tendency for direct development, the hatching individual (seminauta, nauta) acquired a conic or voluted conch with a 1-6 chambered phragmocone and body chamber, with the siphonal division formed. The relict apical opening was a cicatrix. The structure of the shell wall was analogous to that of the mature shell. Both hatching and mature individuals had a swimming behavior. This development type has succeeded in the cephalopod branch by Nautilida (orders Ellesmerocerida, Tarphycerida, Oncocerida and Discosorida) and partly by Orthocerida and Pseudorthocerida, and later by Endocerida and Actinocerida.

In the phyletic branch of the ammonids, belemnites and Recent Dibranchiata, a delay in development evolved. Such a delay was expressed in the protoconch's separation in the embryonal shell, the wall of which consisted of unique microstructure layers. Then a secondary planktonic larva, the deuterocerella (nautella, ammonitella, teutella), developed. The direct development of Recent teuthids is the latest evolutional acquirement.

Thus, I suggest the existence of the following trends in evolution of cephalopod ontogenesis: from a primary larval development to a direct one (Ellesmerocerida, Endocerida and Actinocerida); from direct development to a secondary larval one (within Orthocerida, from Ellesmerocerida – or from Orthocerida– to Bacteritida); from secondary larval to "secondary direct development" (from Belemnitida to Teuthida; from Bactritida – or from Phragmoteuthida – or from Aulacocerida – to Sepiida).

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THE STRUCTURE OF THE SKELETAL ELEMENTS OF EARLY CRETACEOUS AMMONITES AND THEIR SYSTEMATIC IMPORTANCE

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Abstract

The introduction of the scanning electron microscope into the practice of paleontological research has made it possible to study the texture, microstructure and ultrastructure of the skeletal elements of cephalopod mollusks and to clarify their significance in systematics. To pursue this study the shells of 20 genera of early Cretaceous ammonites belonging to 3 orders (Phylloceratida, Lytoceratida and Ammonitida) were studied.

The protoconch of all the ammonites studied was either globular or roller-like in form, with a diameter ranging from 0.25 to 0.8 mm. Its wall consists of 1 prismatic sublayer in the apical portion, and 2 prismatic sublayers in the region where the proseptum is attached to the ventral wall. The wall of the 1st whorl consists of 1 prismatic layer.

The primary varix, which is a thickening of the shell wall, is located at the end of the 1st whorl; its position is defined by "the angle of the primary varix," the size of which ranges from 225 to 340 degrees. It is formed at the expense of the nacreous layer which appears immediately before it or somewhat earlier, remaining very thin at some distance from the primary varix. The primary varix is usually of an ir-

regular lens-shaped form, with a gradual posterior and steeper anterior end. The prismatic layer of the 1st whorl in the primary varix wedges out or curves around its anterior portion. The primary varix is connected with the primary constriction, which is situated immediately beyond the varix, as a rule, and evidenced in various ways in the forms studied: from a hardly noticeable form to a sharply marked one. The height of the whorl usually changes after the primary varix. The primary varix is characterized by marked changes which had occurred in the ontogeny of ammonites; in the opinion of some scientists, it signifies the end of embryonic development (Birkelund, 1967; Ivanov, 1971; and others), while others contend that it stands for the transition from the larval to the postlarval stage (Erben et al., 1968b). We support the former viewpoint.

After the primary varix, the outer wall of the shell of all subsequent whorls consists of 3 calciferous layers (the outer prismatic, the middle nacreous and the inner prismatic layers) and 2 organic layers (the external periostracum and the fine layer lining the shell inside). The calciferous layers do not form at the same time. The outer prismatic and nacreous layers appear on the internal surface of the primary varix in its anterior part, forming the outer surface of the evolute part of the whorl. The inner prismatic layer appears either before the primary varix, or simultaneously with the 2 mentioned above, or on the 2nd whorl of the spiral. In structure, the dorsal wall (the involute part of the whorl) is sharply differentiated from the external (ventral and lateral). It is built out of 1 inner prismatic layer; the 2 other layers, comprising the external wall, wedge out in the area of the umbilical seam. The dorsal wall of the Phylloceratida and the Lytoceratida is thick; in thickness it is either as thick as the ventral wall or thicker by 50-400%. In the living chamber, it wedges out at a distance equal to the length of 1.5-2.5 hydrostatic chambers. The dorsal wall of the ammonites that have been studied was equal in thickness with the ventral wall or thinner; in the living chamber it did not wedge out, but merely thinned. In ammonites with a costate shell, the dorsal wall does not repeat the curves of the preceding ventral wall and forms a smoothed-out inner surface of the shell (*Colombiceras* and *Acanthohoplites*).

Assymetrical bulges, or varices, can be observed in many forms on the 2nd and following whorls, particularly in the Phylloceratida and the Lytoceratida. These varices, just as the primary varix, also develop at the expense of thickening, by 50-400% of the nacreous layer. There may be as many as 10-12 of these varices in the Lytoceratida. The external prismatic layer usually passes the varices without changing, while the inner prismatic layer thins in places of the maximum thickening of the nacreous layer and, quite possibly, wedges out.

A close study of ammonites revealed that the structure of the wall of the protoconch and of the 1st whorl, and the structure of the primary varix and the walls of the shell after it, are closely similar, and this testifies to the common origin of all groups of ammonites.

The first 2 septa – the proseptum and the primarseptum – are of prismatic structure, while the rest are built out of 1 nacreous layer and 2 layers of conchiolin. The mural part of the septa is directed towards the living chamber; at places where the septa are attached to the wall of the shell, a partial "erosion" of the wall takes place, providing for the secure attachment of the septa to the shell. It is fairly possible that, at the same time, a partial recrystallization of this area of the shell wall occurs, particularly marked where the proseptum and primarseptum are located. On the 1st whorl, the septal necks of the Phylloceratida and the Lytoceratida are retrochoanitic; at the beginning of the 2nd whorl they become prochoanitic. In ammonites, prochoanitic septal necks are developed from the 1st whorl.

Short septal necks are typical of the Phylloceratida; long septal necks are characteristic of the Lytoceratida; and short septal necks on the 1st 3 whorls and then short and long necks are typical of ammonites.

A characteristic feature distinguishing the Phylloceratida and the Lytoceratida are special formations – cuffs – encircling the siphuncle. The Ammonitida obviously lack such cuffs. The presence or absence of these cuffs, and the peculiarities of their structure, may be used in defining whether or not an ammonite in question belongs to a given order.

In all ammonites, the siphuncle begins in the protoconch as a drop- or globule-shaped caecum with a diameter from 0.07 to 0.13 mm. The caecum is attached to the wall of the protoconch by means of the prosiphon. The prosiphon consists of a beaker encompassing the caecum and 1 long or several short cords. A long prosiphon is typical of the Ammonitida (it is sometimes attended by several short ones); short prosiphons have been observed in the Phylloceratida and the Lytoceratida. The siphuncle occupies a central position in the 1st 2 septa and then moves to the ventral wall at different speeds. In the Phylloceratida, the siphuncle occupies a ventral-marginal position at the end of the 2nd or on the 3rd whorls; in the Lytoceratida it is in the 1st half of the 1st whorl; in the studied superfamilies of Ammonitida it is in the 2nd-3rd whorls. The change in the position of the siphuncle in the early stages of ontogeny is of systematic importance.

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ON THE COLLECTIVE STUDY OF GASTROPOD EVOLUTION AT THE MESOZOIC–CENOZOIC BOUNDARY

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Abstract

Among the participants of the theme "Evolution and change of the organic world at the Mesozoic-Cenozoic boundary" the following authors worked on the part "Gastropoda": O. V. Amitrov, M. Ya. Blank, V. V. Dzhabarova, L. P. Horbatsch, V. I. Jarkin, T. G. Kalishevitsch, D. E. Makarenko, H. H. Martinson, L. V. Mironova, S. A. Moroz and N. V. Tolstikova.

The work was greatly impeded by the absence of a uniform classification of gastropods, as well as by too small a number of summarizing monographs. Even volume "J" of the *Treatise on invertebrate paleontology* is not yet published. In the main, we follow the system of Wenz (1938-44), and Zilch (1959-60), although with many modifications.

We have analysed (mainly by data from the literature) the distribution of families and genera and changes in their composition in periods, epochs and ages throughout the world, as well as the composition of species of the main gastropod assemblages which existed at the end of the Cretaceous and the beginning of the Paleogene in western Europe and the U.S.S.R. For each geochronological unit, we have counted the absolute numbers of taxa which 1) appeared during this time unit, 2) became extinct in it, 3) existed only in it, etc., as well as the ratio of these numbers to the total number of taxa which existed in the beginning or throughout this time unit. Also, the duration of the unit was considered to define the rate of appearance and extinction of taxa. As a consequence, it became clear that:

1) The family and generic composition of gastropods was changing during geological history (at least during the Mesozoic and Cenozoic) more or less gradually, without any sudden outbursts or extinctions of taxa. Since the Mesozoic, the total number of families and genera has gradually increased until now.

2) In gastropods, the boundary between the Early and Late Cretaceous seems to be more clearly outlined than that between the Cretaceous and the Paleogene. That is due not to the continental groups of gastropods (as in the cases of the land plants, insects, etc.), but to the progressive evolution of marine neogastropods – they had already appeared and flourished in the Late Cretaceous and are prosperous at present. As to the land Pulmonata, many families and genera are known only since the Paleogene; perhaps that is partly because of our insufficient knowledge of the land Cretaceous gastropods.

The similarity (Jaccard's) coefficients of the family and generic composition between the Early and Late Cretaceous is lower than those between any of these epochs and the adjacent epoch of the contiguous period. By generic composition, the similarity between the Jurassic and Cretaceous (periods of the same era) is less than between the Cretaceous and the Paleogene (periods of different eras). For families, the 2 coefficients of similarity are approximately equal.

Only 1 superfamily, the Nerineacea (if not divided into 2-3 superfamilies, as some authors do) died out at the end of the Late Cretaceous. The Euomphalacea, Amberleyacea and Procerithiacea were becoming extinct by the end of the Cretaceous, but their relicts persisted into the Paleogene.

3) In solving the problem of referring the Danian stage to the Cretaceous or Paleogene, it is preferred to include it in the Paleogene since:

A. In this case, the similarity coefficient of the generic composition between the Cretaceous and the Paleogene becomes a little lower, and that between the Jurassic and the Cretaceous becomes a little higher.

B. More families and genera completed their existence in the Maestrichtian than in any other age of the Late Cretaceous; this is the only age in which the extinction of genera outnumbers the appearance of new genera; and in the Danian rather few genera died out, but by the number of newly appearing genera, the Danian gets 1st place among the 9 ages of the Late Cretaceous and the Paleocene.

C. In generic composition (by similarity coefficients), the Danian is closer to the Montian than to the Maestrichtian, and it is closer to the Paleocene, in general, than to the Late Cretaceous.

D. In Europe, species common to the Danian and the Montian are more numerous than those common to the Danian and the Maestrichtian; the latter are completely absent in southern U.S.S.R.

4) When analysing specific composition, one is surprised by the difference of some assemblages, even of the normal marine simultaneous ones (or almost simultaneous ones) and the geographically close and well studied ones. For example, the assemblage of the Montain stratotype near Mons (Belgium) and the one of the Zealand formation of Dania (also of Montian age?) include no common gastropod species at all! Professor M. Gilbert explains it by a little younger age and by the colder-water character of the Zealand fauna.

From data from the literature, most Montian assemblages of the southern U.S.S.R. contain species

common to both Belgium and Dania, but usually with a prevalence for the former (Luzanovka in Ukraine, Crimea, Middle Asia) or of the latter (northern Caucasus, western Siberia). Perhaps these data, after being verified and made more precise, will make it possible to trace the climatic zonation of the Montian seas.

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CHANGES OF ASSOCIATIONS OF FRESHWATER BIVALVES AT THE DEMARCATION OF THE MESOZOIC AND CENOZOIC ERAS, AND CAUSES FOR THESE CHANGES

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Abstract

A study of the faunal changes in space and time is necessary for a knowledge of evolutionary processes of the organic world. The recent paleontological investigation was to accumulate extensive material to throw light on the evolutionary trends of the macrofauna in regions with stable continental regimes. The existence of definite stages in the faunal development was determined. The clearest picture of these changes was observed in the central regions of Asia and North America. On the European continent, where oceanic transgressions occurred repeatedly, the associations of freshwater bivalves were more restricted, as is the case in South America and Australia.

Judging from the basic areals of the freshwater Mollusca, the sharpest change of associations has taken place at the boundary of the Maastriht and the Paleocene.

The majority of fossil freshwater bivalves is included in the order Actinodontida, in the suborder Trigoniina. Three of 7 superfamilies of the latter (Unionoidea, Etherioidea and Mullerioidea) are known in the Mesozoic and Cenozoic eras; the former is represented by the greatest quantity of extinct and contemporary species. The lesser part of the freshwater bivalves is included in the structure of the order Astartida, in the superfamily Pisidioidea. In the Cretaceous and the Paleocene, the representatives of only 1 genus, *Sphaerium*, which have reached our time are known.

Within the limits of the Asian continent (Kazakhstan, Middle Asia, the Far East, Mongolia, China, the Indian Peninsula and Japan), the leading part in the composition of the Late-Cretaceous association is played by representatives of the family Trigonioididae: *Hoffetrigonia, Laotrigonioides, Neotrigonioides, Pseudohyria, Plicatotrigonioides, Buginella* and *Sainshandia*. To the contrary, the Lampsilidae, which existed in Central Asia in subordinate composition, were prevailing in North America. The representatives of the Pisidiidae are in the same situation.

During the Paleocene a considerable renovation of composition of freshwater bivalves was occurring on European, Asian and North American continents. On the Asian continent, the Unionidae, Amblemidae and Margaritiferidae were flourishing, and the Lampsilidae were dying out. In North America, the Lampsilidae were persisting, but by this time the Amblemidae were assuming a greater importance. The Margaritiferidae and Unionidae, extremely poor in genera and species, were inhabiting Europe and North America. The Hyriidae are known in Australia. On the whole, at the boundary of the Senonian and the Paleocene, 7 genera of Trigonioididae were dying out, but 19 new genera of freshwater bivalves were appearing: *Blanfordinaia(?), Indobaphia* (Trigonioididae?), *Ctenodesma, Trapezioideus, Nasus* (Margaritiferidae), *Parreysia, Inversidens, Pressidens, Ensidens* (Amblemidae), *Zaisanunio, Hyriopsis, Lamellidens, Physunio, Pilsbryoconcha* (Unionidae), *Eurynia, Pilea* (Lampsilidae), *Paxyodon, Diplodon* and *Virgus* (Hyriidae).

In contrast to the Cretaceous, in the Paleogene a significant importance of contemporary genera in the faunal complex and a great stability of systematic composition are observed.

The causes of the changes in molluscan associations at the boundary of the Late Cretaceous and the Paleocene are highly diverse. Apparently one of the general causes of such changes was the considerable alteration of physical-geographical characters. The landscapes and climates were changing. In Central Asia, the Laramide-folding phase contributed to a gradual uplift, resulting in the rebuilding of drainage systems over a vast territory. Increased aridity of climate and the reduction of large and spacious water systems led to a dying out of the inhabitants of these basins and to the development of more adaptable Mollusca. In littoral maritime regions, including those in Middle Asia, Europe and North America, the frequent changes of transgressions of sea basins interrupting the successive development of the freshwater

bivalved Mollusca promoted the change of associations of the latter, which were preserved only in the river beds and residual lakes of maritime plains.

The gradual fall of temperatures in the northern region of the terrestrial parts of the globe brought the reduction and disappearance of tropic and subtropic macrofauna, and led to the development of Mollusca of a more temperate climate.

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CHANGES IN THE FAUNA OF BIVALVIA AT THE MESOZOIC-CENOZOIC BOUNDARY

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Abstract

Preliminary results of a joint study have shown that the bivalved mollusks were widely distributed in the Late Cretaceous and Paleocene basins. Representatives of all 3 superorders of the class Bivalvia (according to the classification of Nevesskaya, Scarlato, Starobogatov & Eberzin, 1971) and 13 orders (the 14th order Praecardiida had vanished in the Carboniferous) existed at that time.

Nevesskaya (1972b) ascertained that the Mesozoic-Cenozoic boundary was marked by a "peak" of extinction of superfamilies and, to a greater extent, of families and genera in the Cretaceous. In the Tertiary, the number of new genera and families increased, so that the class became extremely diverse.

An investigation of the systematic composition of Bivalvia for every epoch, beginning from the Late Jurassic until the Eocene inclusive, made these data more precise. It was revealed that the greatest changes in the generic and familial composition occurred in the Late Cretaceous epoch, to which the "Cretaceous peak" of the extinction belonged. The order Hippuritida almost completely vanished, and 21 families and about 300 genera (i.e., nearly 71% of all genera that existed at that time) became extinct.

The presence of the extremely large number of specific genera in the Late Cretaceous, which made up almost a half of all genera which existed at that time, is of great interest, and surely increased the "peak" of extinction. But the maximum extinction of non-specific genera (or declining genera, i.e., those that had lived in the preceding period and vanished in the given time interval) also falls in the Late Cretaceous. In the Early Cretaceous, the number of specific genera was much smaller, and in the Paleocene they were only a few (about 17 and 2%, correspondingly). In the Late Cretaceous, many new genera made their appearance, but almost half of them were specific. Far less non-specific genera (or penetrating genera, i.e., genera which had appeared in a given time interval and survived into the next one) emerged in the Late Cretaceous than in the Paleocene (about 12% of all genera, instead of 33%). It is natural that in the Late Cretaceous the percentage of passing or transit genera was low (17% of the total number of genera), and in the Paleocene it was rather high (about 64%). It is significant that the Recent genera played a rather modest part (21%) in the Late Cretaceous basins; it was approximately equal to that of the mollusks of the Early Cretaceous and the Late Jurassic. And, to the contrary, the percentage of Recent genera sharply increased in the Paleocene (up to 68%).

Thus, at the Mesozoic-Cenozoic boundary (providing that the Danian is referred to the Cenozoic), the general familial and generic composition of bivalved mollusks was greatly changed, mainly due to intensive extinction of genera, and among them to a huge number of specific genera in the Late Cretaceous on the one hand, and to a sharp increase of Recent genera in the Paleocene on the other hand.

According to Jaccard's coefficient, Late Cretaceous bivalved mollusks were closer in generic composition to the Early Cretaceous mollusks than to Paleocene mollusks.

For the present, it is difficult to judge the specific composition of the mollusks at the end of the Mesozoic and the beginning of the Cenozoic. The scope and stratigraphic value of many species should be defined more exactly; their distribution throughout stratigraphic sections remains insufficiently clear. Therefore, in certain cases, exact dating of deposits containing well-studied molluscan faunas (such as the Lusanovkian beds in the Ukraine, the Elburganian horizon in the Pre-Caucasian, etc.) is impossible. All of this impedes the correct evaluation of specific complexes, which were common to one or another time interval. There are certain data on the Crimea (Horbatsch, 1972) and Transcaspian (Panteleev, 1974) where considerably more substantial changes occurred in the composition of specific complexes of bivalved mollusks at the boundary between the Maestrichtian and the Danian, in comparison with those on the Montian-Danian boundary.

Thus, the materials available definitely testify to the great changes in composition of bivalved mollusks which occurred at the Mesozoic-Cenozoic boundary at the end of the Maestrichtian. The period of their intensive extinction in the Late Cretaceous and the time of increased morphogenesis in the Eocene were separated by a whole epoch. This phenomenon seems to be the most likely connected with the change of one or another abiotic factor, and not with the ousting of less adapted forms by better adapted ones.

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CHANGES IN THE CEPHALOPOD FAUNA AT THE MESOZOIC-CENOZOIC BOUNDARY

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Abstract

The end of the Mesozoic and the beginning of the Cenozoic was marked by sharp evolutionary changes within 2 groups of cephalopods (Coleoidea and Ammonoidea) and by very negligible changes in the other (Nautiloidea).

The Nautiloidea are represented by the order Nautilida, which, of all Nautiloidea, includes the largest number of genera and is one of the major orders among fossil cephalopods. Having appeared in the Devonian, the order reached its peak in the Carboniferous-Triassic; at the end of this period, the group became almost completely extinct (according to recent data, only 1 genus survived). A new outburst in the appearance of new species and genera began in the Jurassic and reached its climax in the Cretaceous. In the Paleogene and the Neogene, the group gradually declined, and in Recent seas the order is represented by 1 genus, *Nautilus*, which includes 5-7 species.

Number of taxa in the order

Taxon	Total	D–P	T–K	P–N
Family	30	22	11	3
Genus	ca. 190	ca. 130	62	9-10
Species	1200-1300	ca. 500	ca. 650	ca. 170

One of the most remarkable features of the classification of the Nautilida is its asymmetry – almost 50% of the genera are grouped in only 4 families: Rutoceratidae (Devonian), Trigonoceratidae (Early Carboniferous), Tainoceratidae (Carboniferous-Triassic) and Nautilidae (Jurassic-Present). Together with associated but less voluminous families, they form assemblages which are characteristic of different evolutionary stages of the order. At present, one can distinguish the following stages: Devonian, Carboniferous-Permian, Triassic, Jurassic, Cretaceous, Paleogene and Neogene. About 20 genera (belonging to the families Nautilidae, Pseudonautilidae and Hercoglossidae) are known from the Cretaceous. Most genera are not large. Only *Eutrephoceras* and *Cymatoceras* include a considerable number of species. Eighteen genera have less than 10 species each. The Cretaceous period is actually the time when *Eutrephoceras* and *Cymatoceras* gained dominance. The appearance of *Pseudatureida* at the end of the Early Cretaceous, and of *Aturoidea* (having characteristic sutures with deep and pointed lateral lobes) at the end of the Late Cretaceous was a very interesting evolutionary feature of Cretaceous nautilids. The family Pseudonautilidae (with 5 genera) and 3 genera of the family Nautilidae ended their existence in the Early Cretaceous.

There was no sudden extinction at the boundary between the Cretaceous and the Paleogene. Twelve genera are known from the Late Cretaceous, and 7-8 genera from the Early Paleogene. Two genera (*Deltocymatoceras* and *Carinonautilus*) appeared and became extinct in the Turonian-Campanian, and *Paracymatoceras, Cymatoceras* and *Epicymatoceras* (the latter known only from the Late Maestrichtian) vanished in the Maestrichtian. *Eutrephoceras, Cimonia, Deltoidonautilus, Hercoglossa, Aturoidea* and *Teichertia* survived from the Cretaceous into the Paleogene. *Hercoglossa* and *Aturoidea* appeared in the Maestrichtian, and *Teichertia* in the Danian. The genus *Aturia*, resembling the Ammonoidea in many features, made its appearance in the Early or Middle Paleogene. It rapidly gained a wide distribution throughout the world and became one of the most characteristic genera of the Paleogene and Miocene invertebrates. From the Oligocene of Japan, the monotypic genera *Obinautilus* and *Neocymatoceras* are

known. The origin of the genus *Nautilus* remains unclear; we know a species from the Oligocene whose shell structure is almost indistinguishable from the recent *N. pompilius*.

After the extinction of several genera at the close of the Paleogene, and of the genus *Aturia*, which vanished at the end of the Miocene, the nautiloidean fauna acquired its recent appearance.

At the Cretaceous-Paleogene boundary, the number of species remained almost invariable; it changed considerably towards the Neogene.

Number of species of Nautiloidea in the Cretaceous-Neogene

Region	K_1	K_2	f	N
Europe	ca. 45	ca. 75	ca. 40	7
Asia	ca. 15	ca. 35	ca. 20	3
North America	10-15	ca. 15	ca. 50	1
South America	5	5	ca. 10	1
Africa	ca. 20	ca. 15	ca. 30	4
Australia	—	3	ca. 10	6

(Regions also include adjacent islands.)

The Ammonoidea evolved in a quite different way. Twenty-one families are known in the Senomanian, 23 in the Turonian, 16 in the Coniacian, 12 in the Santonian, 12 in the Campanian and 11 in the Maestrichtian (Moore, 1957). Some new families appeared and became extinct in almost every age, the surviving families prevailing considerably. In the Maestrichtian, things were quite different; the major part of the group died in the 2nd half of the Maestrichtian; only 3 families continued until the end of the Cretaceous.

The findings of the Danian-Paleocene Ammonoidea were reported previously. All such findings are extremely interesting and should be thoroughly studied, since they may be connected both with persistence of small groups of Ammonoidea into the Paleogene and with incorrect dating of the rocks containing these fossils (Naidin, 1972).

At present, it is difficult to judge the evolution of the Coleoidea, since only the Belemnoidea of this large group remain preserved. The last Late Cretaceous Belemnoidea are known from the Maestrichtian. The peculiar genus *Bayanoteuthis*, which is singled out into its own family Bayanoteuthidae, has been described from the Eocene of western Europe. The origin of this group is still not known, but it hardly seems to be connected with the last Mesozoic Belemnoidea (Naidin, 1972).

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REGULARITIES OF MOLLUSCAN EVOLUTION IN CLOSED AND SEMICLOSED BASINS OF EURASIA IN THE LATE MIOCENE AND EARLY PLIOCENE

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Abstract

In Neogene times, the area of Parathetys was characterized by its cyclic geological development, which conditioned repeated changes in the physical-geographic environment and the alternation of different types of basins, among them closed and semiclosed ones. Every cycle usually began with the appearance of a communication between the Ponto-Caspian basin and the normal marine basin, and penetration into the former by a diverse marine fauna, which very soon became widespread. Then the break of this communication followed, which caused a subsequent impoverishment of the fauna, due to the gradual disappearance of polyhaline forms. Euryhaline marine species which had survived the decrease in the salinity of the water became, as a rule, highly variable and gave rise to numerous species and even to genera. Further freshening of the water could stipulate the invasion into the basin of brackish water and fresh water forms which inhabited estuaries and deltas; that was also usually accompanied by vigorous

morphological diversification and species.

Depending on the degree of isolation and decrease in the salinity of basins, and judging from the type of fauna prevailing in them, one can distinguish semiclosed, semimarine, closed semimarine and brackish-water basins. Semimarine basins are characterized by the prevailing marine fauna, and the brackishwater basins are characterized by a dominant fauna of a brackishwater or "Caspian" type, i.e., by those forms which in marine waters could live only if the salinity of the water did not exceed 0.5-5 ‰, or rarely 8 ‰. In brackish water, where sulphates and divalent cations are prevalent, they were tolerant even to much higher salinity. Semiclosed basins are always of the semimarine type, and closed basins are of the brackishwater or, rarely, the semimarine type.

Thorough study of fossil mollusks from basins successively replacing each other (closed semimarine Sarmatian, semiclosed semimarine Early Maeotic, and closed brackishwater Late Maeotic and Early Pontian basins) made it possible to follow the course of the fauna's evolution and its change in the basins of all 3 types.

The composition of the mollusk fauna in semiclosed, semimarine Early Maeotic basins was characterized by the obvious predominance of forms of marine origin. Members of polyhaline genera and species occurred very rarely. This fact proves that communication with the open sea was impeded and not constant. The number of marine genera in proportion to the number of genera from the open Middle Miocene sea shows the same impoverishment of the fauna that is characteristic of the Recent Sea of Azov. At the same time, communication with the normal marine basins, although it was obstructed, seems to hinder speciation, and so no new species of bivalves appeared in the Early Maeotic sea. Among gastropods, only 1 genus and 2 species arose. In the Early Maeotic basin, morphogenesis found its expression only in a very wide range of intraspecific variability, and in some cases in the appearance of new ecological morphs and subspecies.

The mollusk fauna of the Sarmatian basin was also characterized by the prevailing marine forms (which did not include any species of polyhaline genera), as well as by a proper family and generic composition in comparison to the fauna of the preceding open, Middle Miocene basin. But, unlike the Early Maeotic semimarine basin, the Sarmatian semimarine basin was completely closed, and this left a definite mark upon the development of its fauna. Along with wide intraspecific variation of the majority of species and the increase of most euryhaline species in their absolute size, which was also characteristic of the fauna of semiclosed basins, the evolution of Sarmatian mollusks was marked by a more rapid and intensive speciation, which made this fauna highly specific and endemic, and resulted in the formation of fully endemic communities (and among them of deep-sea communities). By the end of the Sarmatian, the distribution of trophic zones usual for inland seas was changed: the zone of the detritus feeders disappeared and sestonophages occupied deeper areas. In closed and semimarine Sarmatian basins, the mollusk fauna evolved in 3 stages: 1) extinction of polyhaline forms and variation of the surviving euryhaline species (in the Early Sarmatian); 2) intensification of species evolution and morphogenesis (in the Middle Sarmatian, a time of optimal development of mollusks); and 3) extinction of all endemic Sarmatian species and the predominance of members of only one genus, *Mactra*, which also became extinct by the end of this age.

The fauna of the closed, brackishwater basins (for example of Late Maeotic and Early Pontian basins) was distinguished by very few marine genera, a wide range of intraspecific variation, intensive species evolution and morphogenesis, as well as by endemic bottom communities and the absence of a zone of detritus feeders.

The analysis has shown that in closed and semiclosed basins the evolution of the fauna acquired certain characteristic features, which can be used as indicators in detecting basins of the same type existing throughout the whole geological history of the earth (some Permian ones, for instance).

The fauna of closed and semiclosed basins may be distinguished by the following features: 1) the scanty number of families and genera in relation to that from the contemporary open marine basins; 2) wide individual and group intraspecific variation; 3) formation of endemic bottom communities; 4) a predominance of euryhaline marine families in semimarine basins; 5) presence of brackishwater forms, which were dominant in the brackishwater basins; 6) in closed brackishwater and semimarine basins, a large number of specific and endemic species, and even genera; 7) in closed brackishwater and semimarine basins, a large number of species in relation to the number of genera, caused by intensive speciation within a few genera; 8) specific distribution of trophic zones, according to bivalve mollusks in particular, disappearance of the zone of detritus feeders in closed basins; and 9) a decrease in absolute size of species belonging to marine, more polyhaline genera, and, in some cases, a certain increase in the size of most euryhaline forms took place in semiclosed semimarine basins. The increase in size of the representatives of specific species in comparison with the species of the same genera from marine basins is characteristic of closed brackishwater and semimarine basins.

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PLIO–PLEISTOCENE MOLLUSKS OF BOREAL REGIONS AND SOME QUESTIONS OF LATE CENOZOIC PALEOGEOGRAPHY

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Abstract

The study of Upper Cenozoic deposits of the northern Atlantic (England, Iceland) and the northern part of the Pacific Ocean (Kamchatka, Sakhalin and adjacent areas), carried out during recent years, enabled a comparative analysis of old mollusk assemblages, the elucidation of some regularities of the change of assemblages in the geological past, and the deciphering of certain characteristics of Late Cenozoic paleogeography. This concerned, to a great extent, characteristics of ecosystems of the past.

It follows from comparison of the assemblages of the above areas that, if in Miocene time they had a negligible percentage of common species, in Pliocene and Quaternary times their number of common forms increased considerably, although endemism of the assemblages remains high enough. The latter points to closer relationships of the North Atlantic and Pacific basins in the Plio-Pleistocene time than in the Miocene period.

An analysis of old assemblages shows that during the Pliocene-Eopleistocene the biogeographical type of mollusk associations in the North Atlantic and in the northern Pacific Ocean regularly changed from south-boreal (Early Pliocene) to boreal (Late Pliocene), north-boreal and arctic-boreal (Eopleistocene-Pleistocene). At the same time, the percentage of extinct species in these assembalges also varied: from 75-80% in the Upper Miocene to 40-45%, 20-25% and 4-8% in the Lower and Upper Pliocene and Eopleistocene, respectively. These directed changes appear to reflect general tendencies in the change of the malacofauna of the past in having a rather global character.

During the Pliocene, a considerable migration of mollusks (the appearance of a great number of boreal forms of Pacific origin) from the Pacific Ocean into the Atlantic Ocean took place through the Arctic basin. In Quaternary times, the Arctic biota was greatly influenced by the northern Atlantic flora.

The Pliocene migration began about 3 million years ago, when the Bering Straits originated. The northern ocean, through which the migration was proceeding, was much warmer than it is now. During the Plio-Pleistocene, the climate was growing noticeably worse, this having been pronounced in the replacement of warm-water assemblages by more cold-adapted assemblages, and the appearance of glacial deposits in the sections. Traces of cooling were observed in the Pleistocene as well, particularly at the level of 3 and 1.8 million years ago.

Dispersion of benthonic forms in the past was greatly influenced by physical barriers (the Bering bridge, the Tule bridge, etc.). In particular, the Tule "bridge" in the North Atlantic appeared to be functioning until the end of the Pliocene. This was expressed clearly enough in the peculiarity of the old North Sea faunas, the exchange of which, with the assemblages of more southern regions, was markedly impeded.

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HISTORY OF THE FAUNAS OF BIVALVE MOLLUSKS OF NEOGENE BASINS OF THE EASTERN PARATHETYS

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Abstract

Bivalve mollusks constitute one of the groups of organisms most widely distributed throughout the world in the Neogene, which allows us to consider them as one of the most significant groups in reconstructing environmental conditions of the past, both within single basins and within areas larger in scale. It is of definite interest to consider the fauna of certain spacious regions, and among them Parathetys, which extended in the Neogene from Yugoslavia in the west to the Aral Sea in the East. To clarify peculiarities of the evolution and changes in the bivalve mollusk fauna (which inhabited Neogene basins of

the eastern Parathetys encompassing southern regions of the U.S.S.R. from the Aral to Moldavia), the stratigraphic and geographic range of all 765 species registered in the Neogene of this area was studied.

The fauna of each successive basin is characterized by the total number of species and genera, as well as by the species-generus ratio and the percentage to the total number of species of 1) species living now, 2) species transferred from the previous basins, 3) species which appeared at a given stage, 4) species which died out at a given stage, 5) species transferred to the subsequent basin, and 6) endemic species.

Analysis of the data obtained permits us to establish the following regularities. The earliest sharp limit in the evolution of the Bivalvia falls into the lower boundary of the Sakaraulian, when the percentage of Recent species rose from 6 to 30%, and remained at this level until the end of the Konkian. Simultaneously with the increase in the number of Recent species at the boundary between the Sakaraulian and the Caucasian, the specific composition was considerably renewed: 58% of the species became extinct, their extinction and corresponding change in the specific composition being in no way caused by obvious environmental alterations, since, judging from the diverse fauna and predominance of polyhaline genera, both basins had a normal marine salinity. The extinction of some species was accompanied by the appearance of others closely related to the extinct species (not less than 25% of the extinct species gave rise to new species).

The onset of the Sakaraulian was marked in the area of the eastern Parathetys by the transgression of the sea, which conditioned a wide prohorese of species from the western regions (among 35 of the early existing species only 15 were in common with the preceding Caucasian basin of the eastern Parathetys).

The Kozachurian basin, which replaced the Sakaraulian basin, was distinguished by a brackishwater fauna of poor specific and generic composition. Therefore, the Sakaraulian stage came to an end with the regression which caused the replacement of marine conditions with those of a brackishwater basin in both eastern and central Parathetys. Due to specific conditions of the basin, the Kozachurian fauna was strictly endemic. The origin of the Kozachurian fauna remains obscure. One part of the species seems to have originated from Sakaraulian forms in the eastern Parathetys, but the other part came from the west.

Next, the Tarkhanian, a stage in the development of the eastern Parathetys, was again marked by transgression of the sea, which advanced from the area of the Mediterranean. Only 2 species were in common with the preceding eastern Parathetic basin. Endemic forms were not numerous, but were more abundant than in the Sakaraulian basin. This shows that the communication with the open seas was somewhat obstructed. In the following Tschokrakian time, the isolation became more pronounced; this is proved by the highly endemic fauna which existed at that time. The overwhelming majority of species were in common with the species from the Tarkhanian basin, or were derived from the latter. The fauna of the Karaganian basin was directly connected with the Tarkhanian-Tschokrakian fauna, which was very poorly represented. Its endemicity was very high, thereby also testifying to the closed nature of the Karaganian basin, although (judging by the rare marine forms found in the upper part of the Karaganian deposits) it could have had a short-term communication with the open seas. The Karaganian closing was more or less united with Tarkhanian-Karaganian times in the development of the eastern Parathetys.

The Konkian transgression brought numerous and diverse marine species; and only a few species came from the Karaganian basin. The endemicity of the Konkian fauna, as well as the species-genus ratio, were rather low. All this indicates that the Konkian basin had a wide communication with the open seas. The end of the Konkian stage signified the starting reservation and distillation of the eastern Parathetic basin. At this time the majority of the polyhaline species disappeared and new species emerged and later produced the diversity of the Sarmatian Bivalvia. Forty-seven percent did not pass over the Konkian (=Badenian) and Sarmatian limits.

In the Miocene of the Parathetys area, 2 sufficiently distinct boundaries were traced in the evolution of bivalved mollusks: 1) the beginning Sakaraulian (=Burdigalian, Eggenburgian) and 2) the boundary between the Konkian (=Badenian or "Tortonian") and Sarmatian. In the eastern Parathetys, 2 more boundaries were traced when the mollusk fauna had been almost completely renewed due to the prohorese of numerous polyhaline forms – in the early Tarkhanian and beginning Konkian. These latter boundaries are of local importance only for the eastern Parathetys. The Konkian (=Badenian)-Sarmatian boundary, which was mainly conditioned by the environmental alterations caused by a vast sea regression, also cannot be considered as an evolutionary one, but, due to its wide extension, it may serve as a definite biostratigraphic marker.

We cannot judge the general changes in the evolution of bivalved mollusks which began during the Late Miocene of the Parathetys, since the basins which communicated widely with the open seas ended their existence here in the Sarmatian. But, nevertheless, successive changes in the fauna of bivalved mollusks yield good information on the palaeographic changes which were taking place in this area. The origin of the Sarmatian malacofauna was directly connected with the fauna of the preceding Konkian basin. It was evolving under the conditions of a basin which had been turning to a more closed and distilled type. By the close of the Late Sarmatian, all Sarmatian species of marine origin died out. The Early Maeotic marine fauna came from some other basin of the area of the Mediterranean and was highly endemic. In the 2nd half of the Maeotic, it became almost completely extinct, the extinction being

caused by the conditions of a brackishwater basin, which by that time had replaced the previous one.

Only a few species passed into the Pontian basin, which replaced the Maeotic basin in the area of the eastern Parathetys. The Pontian fauna was mainly constituted by migrants from the Pannonian area and, to a lesser degree, due to the prohorese of species from the Aegean basin. Thus, in the area of the eastern Parathetys, a great change in the molluscan fauna took place at the boundary between the Maeotic and the Pontian. There came in turn various brackishwater fauna of the Caspian type, which became dominant, and, evolving new species, survived over the area of the Black Sea until the Middle Quaternary. One more boundary was traced in the area of the Caspian Sea, i.e., the appearance, due to sea transgression, of the Akchagylian fauna, a very impoverished fauna of the Mediterranean type. These last 2 boundaries were conditioned by palaeogeographic changes, which caused very significant changes in the molluscan fauna, due to both the prohorese and the evolution of single groups of species and genera.

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BRACKISH- AND FRESHWATER MOLLUSKS FROM ANTROPOGENE DEPOSITS IN THE VALLEYS OF THE INGUL, INGULETS AND SOUTH BUG RIVERS, AND THEIR RELATIONSHIP WITH RECENT MALACOFAUNAS

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Abstract

According to the author's collections and available data from the literature, the Recent malacofauna of the South Bug, including the Bug liman, Ingul and Ingulets, consists of 85 species. In general, they are freshwater organisms, to which are joined Ponto-Caspian and other liman species.

In the freshwater malacofauna of the Ingul, Ingulets, South Bug and their tributaries were found *Lymnaea stagnalis, Radix auricularia auricularia, R. auricularia ampla, R. auricularia fluviatilis, R. auricularia tumida, R. auricularia lagotis, R. ovata ovata, R. ovata obtusa, R. ovata patula, R. ovata fontinalis, Galba palustris, G. corvus, G. taurica, G. turricola, G. truncatula, Amphipeplea glutinosa, Physa fontinalis, Aplexa hypnorum, Planorbis planorbis, Planorbarius corneus, Anisis vortex, A. vorticulus, A. septemgyratus, A. contortus, Gyraulus albus, G. gredleri gredleri, G. gredleri rossmaesleri, G. laevis, Armiger crista, Segmentina nitida, Hippeutis complanatus, Acroloxus lacustris, Succinea putris, S. oblonga, S. pfeifferi, Theodoxus fluviatilis, Valvata piscinalis, V. pulchella, V. cristata, Viviparus contectus, V. viviparus, Lithoglyphus naticoides, Bithynia tentaculata, B. tentaculata producta, B. leachi inflata, Unio pictorum pictorum, U. pictorum limosus, U. tumidus, Crassiana crassa, Anodonta cygnea, A. zellensis, A. piscinalis piscinalis, A. piscinalis ostriaria, A. piscinalis subcircularis, A. ponderosa, Pseudanodonta complanata, Sphaerium rivicola, S. solidum, S. corneum, S. lacustre, Pisidium amnicum, P. supinum, P. henslowanum, P. ponderosum, P. subtruncatum, P. personatum, P. obtusale* and *P. tenuilineatum.*

The role of liman mollusks increases with the approach of the mouths of the rivers. In the Ingulets River, and in its Saksagany tributary, *Dreissena polymorpha* is rather abundant. In the lower part of this river, from the town of Snigirevka and to the mouth, *Hypanis angusticostata angusticostata, Theodoxus euxinus, Fagotia esperi* and *F. acicularis* occur.

The richest liman fauna is in the Ingul River, and especially in its lower part. Here in addition to species occurring in the Ingulets (excluding *Hypanis angusticostata*) *H. pontica, H. colorata* and *Dreissena rostriformis* are encountered.

The most abundant liman fauna is in the South Bug. Thus, *Fagotia esperi* and *F. acicularis* are distributed in the Bug from the mouth to the town of Vinnitsa; *Dreissena polymorpha* is also recorded from this region. From the town of Alexandrovka and further down the river, *Theodoxus danubialis* and *Lithoglyphus pyramidalus* occur.

Theodoxus euxinus was found near the town of Novaja Odessa. In passing from the Bug channel to the Bug liman, *Caspia makarovi, Turricaspia variabilis, T. triton, T. caspia lincta, Hypanis laeviuscula fragilis* and *Dreissena rostriformis* begin to occur, and in the Bug liman itself, *Turricaspia limanica, T. plicata relicta, Hypanis colorata,* and *H. pontica* occur. The bottom deposits of the lower parts of the above rivers consist, to a considerable extent, of empty shells, which either form banks or part of the shell bottom or is mixed with sand or gravel.

In the Ingul and Ingulets, the shell bottom is now covered with silt, the accumulation of which began

in past years due to the ploughing of bottom lands for agricultural purposes. These river bottoms consist of valves and shells of mollusks of freshwater, brackish (liman) and sea complexes. All the species exist now, although not all of them occur in the rivers investigated. The representatives of the liman fauna are most abundant in these deposits (they account for 90% of the valves and shells found). Many of the above freshwater mollusks were found here, and also marine shells were found as well (*Mytilus galloprovincialis, Cardium edule lamarcki, Tritlia reticulata* and *Hydrobia ventrosa*). However, the marine shells are very rare and are much worse preserved than shells of liman mollusks. These deposits coincide, in general, with the Recent distribution of the liman fauna, but a few specimens of liman mollusks were found in higher parts of the river. Thus, in the South Bug near the town of Savran, members of the genera *Caspia* and *Hypanis* were found in the bottom deposits.

The occurrence of these subfossil mollusks over a great extent of the South Bug, Ingul and Ingulets shows that not long ago this territory was covered by the sea, or at least by a large liman-like waterbody, where, to a considerable extent, a liman fauna developed. This waterbody, judging by the abundant brackishwater species, did not have a very high salinity, which allowed some euryhaline marine species to exist.

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FOSSIL LIMNOSCAPHS IN THE SOUTHERN UKRAINE

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Abstract

The genus *Limnoscapha* was established in 1932 by Lindholm. In describing its form, he drew attention to its distinctive differences from representatives of the genus *Unio*, and he supposed that in the future *Limnoscapha* might be distinguished by a separate subfamily, the Limnoscaphinae. However, impressed by the study of Kreyci-Graff & Wenz (1931), where forms from the *maximus* group similar to *L. sulcata* were referred to the genus *Hyriopsis*, Lindholm considered it necessary to regard his genus as a subgenus of *Hyriopsis*. Without changing the text, this was reflected in a palaeontological table. Subsequently, following Wenz, forms similar to the *maximus* group have been referred to the genus *Hyriopsis* (Bolgiu, 1953, and others).

Martinson, in studying the freshwater Mesozoic-Cainozoic fauna of the Asiatic territory of the U.S.S.R., concluded that it was necessary to retain *Limnoscapha* as a genus, because of distinctive differences between *Limnoscapha* and *Hyriopsis*. The independence of this genus has been admitted by Bogatchev, Popova, Jatzko, Starobogatov, Model, and others.

Starobogatov (1970) proposed to subdivide the group of fossil *Limnoscapha* into 2 genera: *Limnoscapha* and *Potamoscapha*. *Hyriopsis kreycii* Wenz 1931 was taken as the type species of the new genus. Wenz, however, referred *Anodonta problematica* Cobalcescu, *Unio pterophorus* Brusina, *U. maximus* Fuchs, *U. fuchsi* Penecke, and provisionally *Anodonta pseudohyria* Sinze and *A. rothi* Lörenthey to the genus *Hyriopsis*. Thus, the content of the genus *Hyriopsis* following Wenz seems to be somewhat uncertain: it includes *Hyriopsis (H. pseudohyria)* and *Limnoscapha (H. kreycii, H. krausi, U. maximus* and *U. fuchsi)* and forms close to the genus *Prohyriopsis* Haas 1914 (*A. problematica*). The latter form was chosen by Starobogatov as the type species for his new genus *Pseudohyriopsis*.

Remnants of *Limnoscapha* are rather abundant in the Late Miocene and Pliocene sediments in the Ukraine. Jatzko (1972) distinguished 2 genera in these fossils, *Hyriopsis* and *Limnoscapha*, based on investigations of Neogene unionids. To *Limnoscapha*, he referred new species close to the *maximus* group (*L. fornicata, L. cagulis* and *L. rossica*), and to *Hyriopsis*, only *A. pseudohyria*.

At present, we have at our disposal a rather rich collection which makes it possible to trace species development in space and to outline some genetic relationships. To the genus *Limnoscapha*, we refer large specimens (up to 23 cm long) with a long egg-shaped shell lacking a wing, with non-prominent umbones, without a subumbonal cavity and with anterior teeth diverging forward and downward. The oldest representatives of this genus in the Ukraine are known from the Upper Sarmatian sediments – *L. fornicata* and *L. rybakovi*. They differ from the later representatives of this genus, in addition to other features, in the absence of rough plications on the shell surface. It must be emphasized that no wing is observed in any specimens examined. The wing is also absent in Maeotic and Pontic shells (*L. bugensis*

Gozhik and *L. jatzkovi*). Pontic representatives of *Limnoscapha* have the most distinct rough plications on the shell surface, which become less distinct and disappear at the end of the Pliocene (in *L. stefanescui*).

To the genus *Potamoscapha* Starobogatov 1970, we refer *Unio maximus, Hyriopsis krausi, H. kreycii, Limnoscapha cagulis* and some new species from the Maeotian and Pontian of the Black Sea region. They differ from *Limnoscapha* s. st. in a long-oval form of shell with originating wing, straighter dorsal margin, pattern of rough plications, greater height coefficient, and position and structure of anterior teeth.

The Early Sarmatian *Potamoscapha* (*P. eduardi* Gozhik and *P. sarmatica*) are of a somewhat distinct position. They are, as a rule, of smaller size, oval-shaped, with small wing, and the shell is more convex and without rough plications. They appear to be referrable to another subgenus.

In conclusion, it should be emphasized that *Limnoscapha* represents a very important group of naiades and, in terms of stratigraphy and palaeobiology, they are more widespread in the Neogene of southern U.S.S.R. than one formerly thought. Regular decrease in abundance of species and their numbers, from the Early Sarmatian to the Pliocene and their extinction at the end of the Pliocene, are revealed in their evolution. The development of rough plications on the shell surface is not a constant characteristic for this group of mollusks. The most developed plications are observed in the Early-Middle Sarmatian, and their complete disappearance is confined to the end of the Pliocene.

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CENOZOIC *GASTROCOPTA* OF EURASIA (GASTROPODA: PULMONATA)

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Abstract

The *Gastrocopta* are one of the most abundant groups of terrestrial snails in Cenozoic sediments, with more than 28 species. Among these, 13 are reported from western Europe, 10 from the Ukraine, 10 from the northern Caucasus Mountains region, 10-11 from the Asiatic part of the U.S.S.R. (the southern Urals, the basin of the Irtysh River, the Balkhash region, Tuva and the Baikal region) and 5 from central Mongolia.

The oldest *Gastrocopta* are found in the Middle Oligocene sediments of western Europe (*G. (Albinula) turgida* Reuss) and Mongolia (5 species of 4 subgenera: *G. (Albinula) mongolica* Prisyazhnyuk, *G. (Kazachalbinula) derraktini* Prisyazhnyuk, *G. (Kazachalbinula) shandgolica* Prisyazhnyuk, *G. (Privatula) primitiva* Prisyazhnyuk and *G. (Sinalbinula)* sp.

The Late Oligocene *Gastrocopta* are known only from western Europe, and, in addition to *G. turgida* Reuss, include 2 species of *Sinalbinula: G. (Sinalbinula) didymodus* Sandberger and *G. fissidens* Sandberger.

Almost the same species are characteristic of the Early Miocene. *Gastrocopta turgida* Reuss and *G. fissidens* Sandberger are already present, and *G. (Sinalbinula) obstructa* Sandberger appear.

The onset of blossoming of *Gastrocopta* (which can be explained by taxonomic features, or perhaps by a more detailed study of the occurrences) was in the Middle Miocene. In western Europe abundant species of *Albinula* appear – *G. acuminata* Klein and several species of *Sinalbinula: G. farcimen* Sandberger, *G. ferdinandi* Andreae, *G. nouletiana* Dupuy and *G. gracilidens* Sandberger. Also dwelling there were *G. (Albinula) turgida* Reuss and *G. (Sinalbinula) obstructa* Sandberger. At that time in the Ukraine and in the northern Caucasus Mountains region, western European species were spread, with the exception of *G. turgida* Reuss and *G. obstructa* Sandberger.

On Asiatic territory (Balkhash region, Tuva), the following are widespread in the Middle Miocene: subgenus *Kazachalbinula* (*Gastrocopta kazachica* Steklov), specific *Albinula* which distinctly differ from western European forms (*G. krestnikovi* Steklov) and specific *Sinalbinula* similar to *G. nouletiana* Dupuy and *G. obstructa* Sandberger (i.e., *G. gemina* Steklov, *G. tuvaense* Steklov, *G. intorta* Steklov, *G. perfida* Steklov, *G. subtuvaense* Steklov, *G. conturbata* Steklov and *G. (Sinalbinula)* sp.). In the Balkhash region, only 1 European species, *G. nouletiana* Dupuy, occurs.

In the Late Miocene, the situation did not change very much. In western Europe many Middle Miocene species continued to exist, which underwent changes at the subspecies level, and also *Gastrocopta (Sinalbinula) suevica* Sandberger appeared. At that time, in the Ukraine and in the northern Caucasus

Mountains, western European species were predominant; but the following also occurred: *G. (Albinula) steklovi* Prisyazhnyuk, similar to tuvinian *G. krestnikovi* Steklov, *G. (Sinalbinula) pseudotheeli* Steklov, and specific *Kazachalbinula: G. ukrainica* Steklov, *G. subzamankulense* Prisyazhnyuk and *G. (Kazachalbinula)* sp.

Additionally, rare occurrences of *Gastrocopta (Albinula)* ex. gr. *turgida* Reuss are recorded in the Late Sarmatian of the southern Ukraine.

The Early Pliocene *Gastrocopta* were studied only from western Europe; the occurrences of *Albinula (G. acuminata* Klein) were displaced to the south (Austria and Hungary), and gradually approached the Mediterranean Sea. At the same time, the endemic species *G. (Albinula) edlaueri* Wenz was distributed. *Sinalbinula* is represented by *G. nouletiana* Dupuy and *G. fissidens infrapontica* Wenz. In the Ukraine, only *G. nouletiana* Dupuy, *G. gracilidens* Sandberger and *G. fissidens* Sandberger are found.

The Late Pliocene *Gastrocopta* differ rather distinctly from the older ones. Varieties of European *Albinula*, *G. acuminata fossanense* Sacco and *G. turgida guattuordentata* Sacco, are known in the Mediterranean region. In France, endemic *G. (Albinula) dupuy* Michaud dwelled at that time. Only several representatives of *G. nouletiana* Dupuy are known of *Sinalbinula* in the Late Pliocene. During the same time, a single species similar to *G. nouletiana* Dupuy is reported for the Ukraine; in the region of the northern Caucasus Mountains, where terrestrial mollusks are better studied, the following are found: *G. (Kazachalbinula) zeamankulense* Steklov, *G. subzamankulense* Prisyazhnyuk; *G. (Sinalbinula) gracilidens* Sandberger (close to the Upper Miocene ukrainian species and also known in the southern Urals), and the specific (possibly endemic) *G. (Sinalbinula) calumniosa* Steklov.

In the Asiatic part of the U.S.S.R., *Gastrocopta gracilidens* Sandberger and the Recent *G. (Sinalbinula) huttoniana* Benson always occur.

An analysis of the geographic and stratigraphic occurrences of Cenozoic *Gastrocopta* shows that 2 major areas of distribution existed for them in the Late Palaeogene and Neogene – Central Asia and western Europe, where the areas of many subgenera and species were confined. For the central Asian area, the development of *Kazachalbinula* and specific *Albinula* and *Sinalbinula* (the substitutes for the European *G. (Sinalbinula) nouletiana* Dupuy) are characteristic. For the western European area, the presence of the group of *Albinula, G. turgida* Reuss and *G. acuminata* Klein, and the group of *Sinalbinula, G. nouletiana* Dupuy and *G. obstructa* Sandberger is characteristic.

The Ukraine and the areas of the northern Caucasus Mountains represent the boundary regions, to which were restricted the margins of the areas of *Kazachalbinula* and European *Albinula* of the group *Gastrocopta turgida* Reuss. The presence of different areas, as far as was permitted in the Palaeogene, refutes the conclusion of Steklov and others about the existence at the same time of a united tropical fauna of terrestrial snails.

Beginning with the Oligocene, and perhaps earlier, species of terrestrial mollusks had their areas of distribution, which, in course of time, could be significantly displaced in space.

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TAXONOMIC COMPOSITION OF FOSSIL BIVALVES OF LATE PERMIAN AGE FROM THE MIDDLE PECHORA REGION

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Abstract

For the purpose of establishing the species composition of bivalve faunas in the Upper Permian lagoon sediments of the Middle Pechora region, the author carried out a layer-by-layer sampling of 60 occurrences of Upper Permian fauna during 1965-70 (the sequences of rivers were: B. Synia, Vjertnaya, Perebora, B. Patoka, Tschugora, Pechora, B. Sopliasa, Osinovka and others). In total, more than 5,000 shells were collected. These belonged to 53 species (of which 11 represented new species, which are absent from the list given below). These species were *Palaeomutela krotowi* Netschajev, *P. stegocephalum* Netschajev, *P. meraca* Betekhtina, *P. monstruosa* Gusev, *P. corpulenta* Gusev, *P. visenda* Gusev, *P. attenuata* Gusev, *Anthraconaia castor* (Eichwald), *A. rhomboiden* (Netschajev), *A. obunca* (Netschajev), *A. oblonga* (Belova), *A. vorcutica* (Pogorevitsch), *Abiella suborvata* (Jones), *A. nana* Khalfin, *A. elliptica* Khalfin, *A. cyclos* Khalfin, *A. ovata* (Betekhtina), *Concinella concinna* (Jones), *C. gravis* Papin, *C. concinnaeformis*

Pogorevitsch, *C. angulata* Pogorevitsch, *Mrassiella sera* Khalfin, *Anthraconauta pseudophillipsii* Fedotov, *A. pseudophillipsii* var. *acuta* Khalfin, *A. supraphillipsii* Khalfin, *A. propingua* Khalfin, *A. gibbosa* Betekhtina, *A. mrassiellaeformis* Betekhtina, *A. tschernyschewi* Khalfin, *A. subacuta* Pogorevitsch, *A. iljinskiensis* Fedotov, *A. simplex* Khalfin, *A. subparallela* Khalfin, *A. obliqua* Khalfin, *A. lata* Khalfin, *A. degeniaensis* Betekhtina, *Sinomya gemina* Pogorevitsch, *S. bella* Gusev and *S. gracilanta* Gusev.

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SPECIALIZATION OF TROPHIC RELATIONSHIPS IN THE SYSTEM "MOLLUSKS – PARASITE OR PREDATOR" AS A PRINCIPLE OF BIOLOGICAL CONTROL OF MOLLUSKS, INTERMEDIATE HOSTS OF HELMINTHS

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Abstract

The problem of biological control of mollusks, intermediate hosts of pathogenic helminths of animals and man, as well as pests of plants, has recently acquired an important role. This can be explained partially by the undesirable after-effects of the use of chemicals. The success of the use of any species in the control of mollusks depends generally, in our opinion, on the specificity of trophic relationships of this species. When speaking about viruses, bacteria, spirochaetes, fungi or protozoans, it would be true to speak about the specific pathogenecity or virulence in relation to mollusks. The specificity of trophic relationships can be considered only in the system "mollusk (prey) – specialized parasite or predator." The more distinct the specificity, the more adequate is the parasite or predator for biological control of mollusks.

Common habitats, community of biotopes and ecological conditions play an important part on a macroscale, since otherwise mollusks are not the preceding link in the food chain for organisms of the 2nd part of the system, but play a secondary facultative role. In searching for organisms for biological control of mollusks, this condition has not always been observed in experiments, since the predator or parasite is offered only one kind of food in the experiment, mollusks. Under such artificial conditions, a parasite or predator consumes the mollusk, and on this basis an ungrounded conclusion is drawn about the possibility of the use of this species for the control of mollusks. The specificity of the feeding of each species of parasite or predator must be defined by the selectivity of the mollusks, the frequency of their occurrence in the stomachs of large species, and by immunological reactions (precipitation) establishing the degree of the relationship of this organism with the mollusks. The necessary specificity of trophic relationships in searching for organisms for biological control of mollusks is, from our point of view, the main and decisive condition for initial investigations.

Recently it has become clear that only the biological control of mollusks cannot solve the problem, and that an integrated method would be more advantageous.

The attractant method of control can also be successfully applied, and attractants can be regarded as an artificial link in a food chain. Bran is a food preferred by mollusks and this can be used as an attractant. When granules of 5% metaldehyde were used in southern Kirghizia for the control of *Xeropicta candaharica*, an intermediate host of protostrongylids, the larvae of flies of the Sarcophagidae were observed to consume the dying mollusks. The same phenomenon was observed in cases with *Succinea putris* in the Kalinin region in experiments using the same preparation. These examples confirm the possibility of an integrated control of mollusks which are intermediate hosts of helminths.

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THE ROLE OF THE SINO-INDIAN ELEMENT IN THE FRESHWATER GASTROPOD FAUNA IN THE DISTRIBUTION OF TREMATODES IN THE SOUTHERN U. S. S. R. FAR EAST

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Abstract

During 1972-73, a study was carried out on freshwater gastropods in the southern Soviet Far East and on their role in the life cycles of various trematode species. Given below are the results of these studies for ascertaining the intermediate hosts of helminths among mollusks belonging to the Sino-Indian elements of freshwater gastropods, which were found in the Amur River drainage (Amur, Khabarovsk and Primorsk regions), as well as in drainages of the Soviet Pacific coastal region.

Mollusks of the Sino-Indian group in the region in question are, as a rule, represented by eastern Asiatic genera (Starobogatov, 1970), their distributions being restricted to the lowest flood lands of the Amur River and its tributaries, and also to the Lake Khanka basin and the Razdol'naya (formerly Sujfun) River in the southern Primorsk region. Mollusks of this group include all species of the family Viviparidae (among which the most abundant are *Cipangopaludina ussuriensis* (Gerstfeldt) and *C. sujfunensis* Moskvicheva), and also species of the genus *Amuropaludina* (*A. praerosa* (Gerstfeldt), *A. pachya* (Bourguignat) and *A. chloantha* (Bourguignat)). Representatives of the 1st genus live in stagnant, weak-flowing, non-freezing waters with abundant aquatic plants. Representatives of the 2nd genus live in river beds and small branches with arenaceous-silty bottoms and slow currents. The family Planorbidae is represented by the genera *Helicorbis* and *Polypylis*, of which the species *H. sujfunensis* Starobogatov and *P. semiglobosa* Moskvicheva are widespread and predominate over other species of Palaearctic Planorbidae in most floodland basins. *Parafossarulus manchouricus* (Mousson) (Bithyniidae) and *Culmenella rezvoji* (Lindholm) (Bulinidae) are also widespread, being most abundant in basins of the middle course of the Amur River and in the Lake Khanka basin.

The mollusk species mentioned above have been examined for partenites, cercariae and metacercariae of trematodes in basins of Lake Khanka and the rivers Ussuri, Razdol'naya, Toungouska, Bira, Bureja and Leya, as well as in the separate regions of flood lands of the middle and upper Amur River course. Considering the role of Sino-Indian mollusk complexes in life cycles of trematodes, one can reveal some characteristic features of their influence on the formation and distribution of the trematode fauna in the southern Far East.

All species of this group are intermediate and supplementary hosts of helminths, cosmopolites and palalarcts. They substitute completely for the absent species or occur together with existing species of molluscan genera which are characteristic of different Palaearctic regions. Biological cycles of trematodes of the family Echinostomatidae (of which *Echinoparyphium recurvatum, Hypoderaeum conoideum* and *Echinostoma revolutum* are of most important epizootological significance) are connected with mollusks of the genera *Cipangopaludina* and *Amuropaludina*, and the species *Helicorbis sujfunensis. Culmenella rezvoji* also takes part as a supplementary host of *E. recurvatum.* Mollusks of the genus *Cipangopaludina* are hosts of trematodes of the family Notocotylidae and, in particular, of *Neudiplostomum attenual* (the parasite of domestic and wild water fowl and hens). *Cipangopaludina ussuriensis* has been noticed as the intermediate host for trematodes of the genus *Azygia* (Mamayev & Oshmarin, 1971) and *Neudiplostomum* sp. *(spathyla?).* A high contamination of trematodes of the suborder Strigeata (*Alaria alata, Cotylurus cornutus, Apharyngostrigea corni, Posthodiplostomum,* and others) by partenites and metacercariae has been found in *Helicorbis sujfunensis* and *Polypylis semiglobosa.* Both species take part in life cycles of trematodes of the family Sanguinicolidae, whereas *H. sujfunensis* plays the main role in spreading paraphistomatosis, one of the most important helminthoses of ruminant animals. This same mollusk is an intermediate host of *Diplodiscus sphincteristoma,* which is a parasite of amphibians. All mollusks of the Sino-Indian complex demonstrate the presence of larvae of different species of plagiorchids, which are distributed in considerable areas of northern Asia and Europe.

The presence of eastern Asiatic mollusks determines the distribution of helminths in the southern Soviet Far East, and were referred to by Oshmarin (1963) as the Indo-Malayan faunistic complex. Research on intermediate hosts of the trematodes *Clonorchis sinensis, Ogomocotile pygargi* and *Asymphilodora japonica,* the distributions of which are connected with southeastern Asia, has shown that their penetration into the Amur River drainage is due to their specific relationship to the genus *Parafossarulus* (represented in this territory by *P. manchouricus*). The solution to this problem requires further study of the biology of trematodes, and particularly of their intermediate hosts.

The data obtained enable us to determine the role of the Sino-Indian freshwater gastropod complex in spreading trematodes, as well as the composition of intermediate and supplementary hosts of trema-

todes, and to understand some aspects of their specificity in relation to different mollusk species. This is of great significance in the organization of preventive measures against helminths in the Far East.

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SHELL STRUCTURE OF MOLLUSKS AND ITS VALUE IN PHYLOGENY AND CLASSIFICATION

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Abstract

Adequate comparison of Recent and fossil mollusks on the basis of their structure and composition creates new possibilities for clarifying problems of evolution and classification.

A 2-layered structure with an outer simple prismatic layer and an inner nacreous layer is now almost proved to be the most primitive type of structure for a mollusk shell. Such a structure reflects the original simple differentiation of the mantle epithelium and is common to those monoplacophorans (Erben et al., 1968a), most ancient bivalves, archeogastropods and cephalopods studied.

There are 2 contrary tendencies in further evolution of shell microstructure: 1) additional differentiation of secretory parts of the epithelium (the number of shell layers being increased to 3, rarely 4, in some neogastropods, pulmonates and freshwater bivalves); 2) reduction of secretory activity to complete elimination of 1 of the primary secretory parts of the mantle epithelium.

In further evolution, simple microstructures rich in organic components had a tendency to change into specialized ones such as crossed-lamellar and "homogeneous" structures, in which the organic matrix part constitutes a few hundredth parts of 1%.

By such a common evolutionary trend, similar types of microstructure could be developed within remote phylogenetic lines. For example, the crossed-lamellar structure is characteristic of several Pectinidae and Limidae, as well as of most heterodont Bivalvia, Scaphopoda and Meso- and Neogastropoda. It shows that the possible trends in structural variations were rather restricted. However, structures identical at the microstructural level are frequently distinguished by their ultrastructural and textural features. It has been well demonstrated by the nacreous structure of different classes of mollusks (Gregoire, 1967; Wise, 1972; Mutvei, 1972) and the crossed-lamellar structure of the Bivalvia and the Gastropoda (MacClintock, 1967).

The shell structure of the Bivalvia is the most diverse; the gastropod structure is more monotonous, and the Cephalopoda inherited the most primitive types of microstructure (the nacreous and simple prismatic types).

The considerable structural modification in the cephalopods reflected the change of parts of the mantle epithelium which produced the shell and reduced the degree of calcification, especially in the Ammonoidea and Endocochlia.

A study of shell structure permits the clarification of certain previously debatable problems of classification (Kennedy et al., 1970; Oberling & Boss, 1970; Taylor et al., 1969, 1973). At the same time, data on the shell structure of bivalves from the literature are not very complete. Thus, it has been considered that the shell structure of the heterodont bivalve family Cardiidae was uniform, and similar in structure to the other 14 families of Bivalvia. A detailed study of more than 150 species of 62 genera and subgenera of the Cardiidae revealed 4 types of shell structure. The subfamily Cardiinae is distinguished by the most simple 2-layered shell, which is formed by a crossed-lamellar outer layer and a complex crossed-lamellar inner layer. The same structure secondarily appeared in Neogene brackishwater cardiids of the subfamily Lymnocardiinae, due to a reduction of an outer layer in their ancestors. The subfamily Fraginae is characterized by a 3-layered structure made up of the outer composite prismatic, middle crossed-lamellar and inner complex crossed-lamellar layers. The subfamily Protocardiinae also has 3-layered shells. The outer layer has a crossed-lamellar structure like the middle one, but with a different orientation of the lamellae. Some transitional structural features allow us to follow phylogenetic relationships in the evolution of cardiids (Popov, 1976).

When the microstructure of different genera is similar, finer textural patterns may be successfully used for systematic purposes. It has been well demonstrated on the superfamily Ostreacea, which has the uniform foliated type of the structure (Tschelzova, 1969).

To reconstruct mollusk evolution, ontogenetic data on their structural development are of great value. The time and order in which every layer was secreted show the degree of differentiation of the mantle epithelium, and could be used in the determination of phylogenetic peculiarities of fossil groups. The study of belemnitids and Recent *Sepia* has shown that in the rostral parts of these 2 groups there were layers of different structure and origin. These data contradict the adopted idea that belemnitids are ancestral groups of the sepiids and demanded either recognition of their independent origin from the Ectocochlia, or the admission of the existence of an "endocochlian" ancestor with a complete set of shell layers. Structural divergence between sepiids and belemnitids found its expression in the elimination of layers which had different origin and microstructure.

A study of cardiids revealed considerable delay in the process of shell ontogeny. Such a mechanism of expansion of ecological potentials is observed among brackishwater Neogene cardiids of the Parathetys (Nevesskaya, 1972a; Popov, 1976).

The study of shell structure has presented a number of new features that should greatly contribute to solving problems of molluscan phylogeny and classification.

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PHYSICAL AND CHEMICAL METHODS FOR STUDYING GROWTH OF MARINE MOLLUSKS

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Abstract

The study of growth of marine mollusks is usually carried out at the population level and implies distinction of the age group of equidimensional individuals based on their statistical frequency distribution. This method is, however, not sufficiently reliable, due to individual growth-rate variation.

Direct observations of growth under natural or laboratory conditions are under way, but they demand much work and time.

The structure and composition of mollusk shells relate to many specific features of their biology, and therefore recently physical and analytical methods have become more and more useful in studying shell substance in terms of growth regularities.

The study of individual growth dynamics of mollusks in relation to their environment, based on the analysis of index-elements in growth layers of the shell, is of special interest. Judging from the study of certain abundant species of Bivalvia and Gastropoda in the Far East, the most effective results are achieved by using combined physical-chemical methods.

Microscopic study of mollusks and computer treatment of data. Structure of mollusk shells and their growth layers were examined on acetate sheets under a microscope in parallel light with x40-300 magnifications. According to structural and external marks of the shells of *Spisula sachalinensis, Glycymeris yessoensis, Mercenaria stimpsoni, Peronidia zyonensis, Raphia vernicosa, Collisella cassis*, and others, the growth layers of different orders (daily, semi-monthly, monthly, annually) have been distinguished. The study of rate variation of individual growth was based on dimensional measurements of each layer. The following rhythms of growth have been revealed from a computer controlled statistic treatment: 7-8 and 13-14 day rhythms for *Mizuhopecten yessoensis* and *Spisula sachalinensis*, ½-month and 1-month rhythms for *Chlamys eritrocomatus*, and 11-15 year rhythms for *Crenomytilus grayanus, Modiolus modiolus*, and others.

The periodicity of growth of the species examined seems to be correlated with the high tide-low tide periodic changes of solar activity.

Oxygen isotope mass-spectrometry. The oxygen isotope content in shell carbonate was determined by the method of decompensation in a Soviet MI-1309 mass-spectrometer. Variations of O^{18}/O^{16} in shells of *Swiftopecten swifti, Mizuhopecten yessoensis, Chlamys nipponensis* and *Collisella cassis*, alongside data on the shell structure, made it possible to ascertain the age of the animals, seasonal and polyannual changes of growth rates, the thermal range within which shell growth takes place, and the dependence of growth rate on environmental conditions. In some cases, optimal temperatures of growth and species temperature specifics were determined. Optimal temperatures of growth for *Swiftopecten swifti* remained invariable from Pliocene up to the present, which indicates the stability of this physiologic-ecological feature.

Spectral analysis and flame photometry. The analysis of seasonal changes of a series of elements (Mg, Sr, Na and Fe) confirmed the annual growth of layers of shells, determined by the structural marks on shells of *Crenomytilus grayanus, Callista brevisiphonata, Mya arinaria* and *Siliqua alta.* The data obtained appear to indicate a distinct tendency of Mg and Sr to increase in calcitic shells, with a rate increase in their formation. However the dependence of Mg content in calcite upon temperature is linear only in the 1st approximation. The study of temperature conditions on growth according to content of these elements demands the elaboration of specific scales for each species.

Complexionometric titration. The determination of Ca and Mg contents (by titrating with a 0.02% solution of trylon B from a 10 ml microburette) were made on calcitic samples from successive growth layers on the shell surfaces of *Mizuhopecten yessoensis, Swiftopecten swifti* and *Chlamys nipponensis.* According to the number of complete magnesium cycles, the age of the mollusks studied was determined: for *S. swifti* with a length of 125 mm, it was 7.5 years; for *M. yessoensis* with a length of 158 mm, it was 5 years; and for *C. nipponensis* with a length of 99 mm, it was 4.5 years. These conclusions are in fairly good agreement with the number of annual rings on the shell surfaces.

It was shown that the distribution of Ca/Mg ratios in shells is caused by the origin of species and by the formation during evolution of a mechanism of stable accumulation of the elements within optimal range of growth conditions. On the other hand, such a distribution seems to reflect the adaptation of mollusks to different unfavorable conditions (low temperature, delay of spawning, etc.).

Further progress in studying shell growth can be accomplished by the application of scanning electronic microscopy and laser microanalysis.

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MALACOLOGICAL REVIEW, P. O. Box 420, Whitmore Lake, Michigan 48189, U.S.A.

NEWS AND ANNOUNCEMENTS

* * * * *

WESTERN SOCIETY OF MALACOLOGISTS. – The 1978 meeting of the Western Society of Malacologists will be held at the University of Santa Clara, near San Jose, California, 28 June through 1 July. Presentation of papers concerning mollusks and other invertebrates will be complemented by field trips, workshops and displays. A symposium concerning current studies of American land mollusks is also scheduled. A 2nd symposium on research dealing with freshwater mollusks is probable. Inquiries about the meeting should be directed to Dr. Peter N. D'Eliscu, W.S.M. President, Department of Biology, University of Santa Clara, Santa Clara, California 95053. Applications for membership should be sent to the W.S.M. Treasurer, Mrs. Carol C. Skoglund, 3846 E. Highland Avenue, Phoenix, Arizona 85018. Annual dues are US $7.50 for regular members, US $1.00 for each additional family member and US $3.00 for student members. Regular and student members receive the *Annual Report* of the Society. – EUGENE COAN

THE AMERICAN MALACOLOGICAL UNION, INC. – The 44th annual meeting of the American Malacological Union (AMU) will be held on 16-21 July, 1978, at the University of North Carolina at Wilmington (UNCW), Wilmington, North Carolina. The program will include contributed papers, symposia, exhibits, and a workshop on methods for building a scientifically valuable shell collection. Field trips which will be available include: 1) SCUBA diving at an artificial reef in the ocean; 2) naiad collecting at Lake Waccamaw; 3) canoe trip from the headwaters of the Waccamaw River through Green Swamp; 4) boat trip to an island with undisturbed Eocene fossils; and 5) boat trip to a barrier island for marsh and dune collecting. Trip costs will vary and some will be limited in number of participants. Membership is open worldwide; however, anyone interested may attend the meeting and present a paper by paying the necessary registration fees.

The price for air-conditioned UNCW dormitories and meals in the University cafeteria is $15 per day per person. Rates are also being arranged for room without board. There are various restaurants on the campus; both budget and luxury motels may be found within a mile of campus. Campgrounds are nearby. Since Wilmington is a coastal city and July is the height of tourist and convention seasons, early motel reservations are recommended. For reservation forms write AMU, Box 394, Wrightsville Beach, North Carolina 28480.

THE CONCHOLOGICAL SOCIETY OF GREAT BRITAIN AND IRELAND, SUMMER PROGRAM FOR 1978. – Field meetings, organised by Mr. T. Pain, 47 Reynolds House, Millbank, London SW1P 4HP, are as follows:

Marine and non-marine meeting to survey the molluscan fauna of Foulness Island – 2 April
Marine meeting to Rhosilli, Gower – 5-7 May
Joint meeting with the Basildon Natural History Society to visit nature reserves in S.E. Essex – 28 May
Fossil and non-marine meeting – 10 June
Joint meeting with the Ipswich Geological Group to look at the Red Crag – 10 June
Non-marine joint meeting with the Northampton Natural History Society – 25 June
Joint meeting with the Yorkshire Naturalists Union – 1-2 July
Marine meeting in Rye Harbour, Sussex – 15 July
Non-marine joint meeting with the Kent Field Club in Dover, Kent – 3 September
Non-marine meeting to visit ancient woodland in East Leicestershire – 23 September
Non-marine meeting in Bedfordshire – 22 October

The following field meetings are being held in various parts of the country, and Members are cordially invited to attend as guests of the organising Society.

Yorkshire Conchological Society: River Ouse at Asselby Island to look for *Succinea oblonga*, 8 April; South House Pavements Y.N.T. Nature Reserve, 6 May; Brigg for fossils, 9 September; Reynards Ings, near Otley, 7 October. For details please contact Mr. A. Norris, City Museum, Municipal Buildings, Leeds.

Northamptonshire Natural History Society: Regular Sunday field trips are held throughout the year. Anyone who would like to join one of these outings please contact Mr. Gordon Osborn.

Bedfordshire Natural History Society: An intensive study of the natural history of Maulden Wood is being conducted. Any Member who would like to visit Bedfordshire on a Sunday please contact Mrs. E.B. Rands.

SOCIETÀ MALACOLOGICA ITALIANA. – The 4th meeting of the Italian Malacological Society will be held in Siena on 6-9 October 1978. The program is as follows.

- 6 October: The opening of the meeting at the Academia dei Fisiocritici, with visits to the historical rooms of the Academia and to various molluscan collections (6:00 p.m.)
- 7 October: Lectures on "The Malacocoenoses" (8:30 a.m.)
  Symposium on the "Biology of Reproduction in Molluscs (4:00 p.m.)
  Documentary films on Siena and its "Palio" (9:00 p.m.)
- 8 October: Free lectures on morphology and systematics (8:30 a.m.)
  Free lectures on ecology and evolution (4:00 p.m.)
  Congress dinner at the Contrada della Chiocciola (9:00 p.m.)
- 9 October: Excursion to the island of Montecristo (Tuscan Archipelago) (7:00 a.m.)
  In the evening the meeting will end.

For further information, write to the President of the organizing committee, Dr. Folco Giusti, c/o Istituto di Zoologia, Via Mattioli 4, 53100 Siena, Italy.

MALACOLOGICAL SYMPOSIUM, SYDNEY, AUSTRALIA. – A "Symposium on the biology and evolution of Mollusca" will be held at The Australian Museum in Sydney for 4 days in May 1979. The symposium will deal with current research in evolution, biology, biogeography, ecology and taxonomy. Further information can be obtained by writing to the organisers, Dr. W.F. Ponder, Department of Malacology, The Australian Museum, P.O. Box A285, Sydney South, N.S.W. 2000, *or* Dr. A.J. Underwood, Department of Zoology, School of Biological Sciences, University of Sydney, Sydney, N.S.W. 2006, Australia.

SYMPOSIUM FRANCO-ANGLAIS SUR LA BIOLOGIE DES MOLLUSQUES DE L'OCEAN ATLANTIQUE. – Ce Symposium organisé par la Société Française de Malacologie et la Malacological Society of London sera placé sous les auspices de l'Université de Bretagne Occidentale, mais se tiendra au Palais des Arts et de la Culture de la ville de Brest, 26-28 Septembre 1978.

Le 1er et le 3éme jour seront consacrés à des interventions d'une demi-heure (20 minutes d'exposé, 10 minutes de discussion). Pendant le 2éme jour, on pourra participer à des discussions informelles ou à l'une des deux excursions suivantes: 1) Brest-Argenton (Ecloserie d'Ormeaux) - Roscoff (Station Marine et Aquarium) - Tinduff (Nurserie de Bivalves); 2) Brest-Ouessant (intérêt touristique).

Les orateurs des 2 Sociétés parleront dans leur langue mais, pour faciliter la compréhension réciproque, un résumé dans l'autre langue sera projeté sur écran pendant la communication. Si vous désirez participer aux exposés en français, vous êtes priés de vous adresser au Secrétariat du Symposium, Laboratoire de Zoologie, Faculté des Sciences, 6, Av. le Gorgeu, 29283 - Brest Cedex, France.

Les conditions d'hébergement et le programme seront annoncés dans une 2éme circulaire. Celle-ci sera envoyée à ceux qui auront rempli la fiche d'inscription provisoire ci-joint, avant le 15 mars 1978. – A. LUCAS and T.E. THOMPSON

TWO NEW RESEARCH STATIONS IN FRENCH POLYNESIA. – Two new research stations have been created in French Polynesia, under the auspices of the Museum National d'Histoire Naturelle and the Ecole Pratique des Hautes Etudes, Paris, for work on a project studying reefs and lagoons, French Polynesia, 120 islands (36 volcanic and 84 atolls); the studies are integrated in a large interdisciplinary and interorganisms program on ecology and rational use of island ecosystem (Man and Biosphere (MAB) program of UNESCO). The Moorea-Tiahura station is located on Moorea Island, 25 km NW of Tahiti, in the Society Islands; it has been operating since 1 July 1972. The station is mostly intended for ecological field research rather than for laboratory investigations. The Hiva-Oa-Taaoa station is located on Hiva Oa Island in the southern group of the Marquesas archipelago; it opened on 1 March 1975. It is intended mostly for field studies, especially land studies, but material is available for marine research.

Research programs include: a) program on establishing the productivity of reefs and lagoons; b) interdisciplinary program on ecology and rational uses of insular ecosystem (MAB Program, Theme 7). Efforts will be concentrated on 2 islands, Moorea (volcanic island) and Takapoto (atoll in the Tuamotus); c) ecological research on *Tridacna maxima* with a view of developing rational utilization of existing resources or artificial culture; d) study of the Vairao reefs and lagoon of Tahiti, concerning the benthic flora and fauna of the lagoon and extending to aquaculture problems; e) study of the pollution and degradation of the Tahiti lagoon, planned to suggest a system of development including the improvement of urban waste product disposal, the protection of soils against erosion and the choice of sites and styles for new construction along the coastlines. – BERNARD SALVAT

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THE WESTERN SOCIETY OF MALACOLOGISTS

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Pomona, California

June 15–18, 1977

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BASTERIA

TIJDSCHRIFT VAN DE

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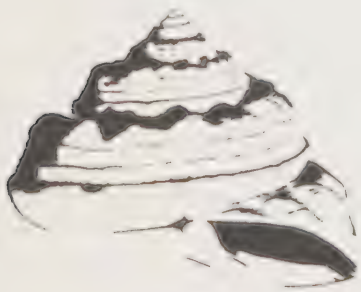

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Sociedad Malacológica del Uruguay

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MOLUSCOS DEL GOLFO SAN MATIAS
(Provincia de Río Negro,
República Argentina)

Inventario y Claves
para su Identificación

por

Víctor Scarabino

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UNIONE MALACOLOGICA ITALIANA

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ELENCO DEI SOCI

al 31 marzo 1977

1 **interessato alle conchiglie marine**
2 **interessato alle conchiglie terrestri e d'acqua dolce**
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4 **interessato alla malacofauna del Mediterraneo**
5 **interessato alla malacofauna mondiale**
6 **gradisce scambi**

Supplemento a «Conchiglie» - N. 3-4 - Anno XIII - 1977

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Bruno Sabelli - Gianni Spada

GUIDA ILLUSTRATA ALL'IDENTIFICAZIONE
DELLE CONCHIGLIE DEL MEDITERRANEO

Fam. **Muricidae I**

Subfam. **Muricinae**	Gen. *Murex*
	Gen. *Hexaplex*
	Gen. *Aspella*
	Gen. *Muricopsis*

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GUIDA ILLUSTRATA ALL'IDENTIFICAZIONE
DELLE CONCHIGLIE DEL MEDITERRANEO

Fam. **Turridae I**

Subfam. **Clavinae**	Gen. *Cymatosyrinx*
	Gen. *Crassopleura*
	Gen. *Spirotropis*
	Gen. *Haedropleura*
	Gen. *Microdrillia*
	Gen. *Drillioia*
Subfam. **Turrinae**	Gen. *Fusiturris*
	Gen. *Lophiotoma*
Subfam. **Turriculinae**	Gen. *Ancystrosyrinx*
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Bruno Sabelli e Gianni Spada
(dell'Istituto di Zoologia dell'Università di Bologna)

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Fam. **Fossaridae** Gen. *Megalomphalus*
Gen. *Fossarus*

Fam. **Capulidae** Gen. *Krebsia*
Gen. *Capulus*

Fam. **Calyptraeidae I** Gen. *Calyptraea*

Bruno Sabelli e Gianni Spada
(dell'Istituto di Zoologia dell'Università di Bologna)

GUIDA ILLUSTRATA ALL'IDENTIFICAZIONE
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Fam. **Naticidae I**

Subfam. **Polinicinae** Gen. *Neverita*
Gen. *Lunatia*

HALIOTIS

1976-VOL-6

COLLOQUE DE DIJON _ mars 1975

POLYMORPHISME ET DIMORPHISME CHEZ LES MOLLUSQUES FOSSILES ET ACTUELS

TROISIÈME CONGRÈS DE LA SOCIÉTÉ FRANÇAISE DE MALACOLOGIE juin 1975

Publié par la Société Française de Malacologie

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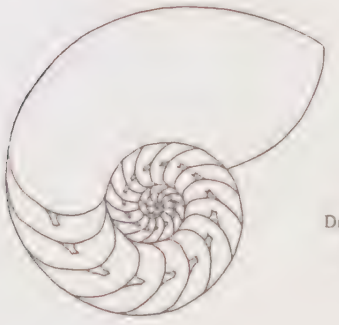

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